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OF THE

American Philosophical Society

HELD AT PHILADELPHIA

FOR

PROMOTING USEFUL KNOWLEDGE

VOLUME LXXIII

1934

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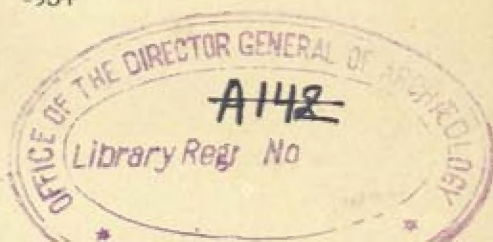
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PHILADELPHIA

THE AMERICAN PHILOSOPHICAL SOCIETY

1934



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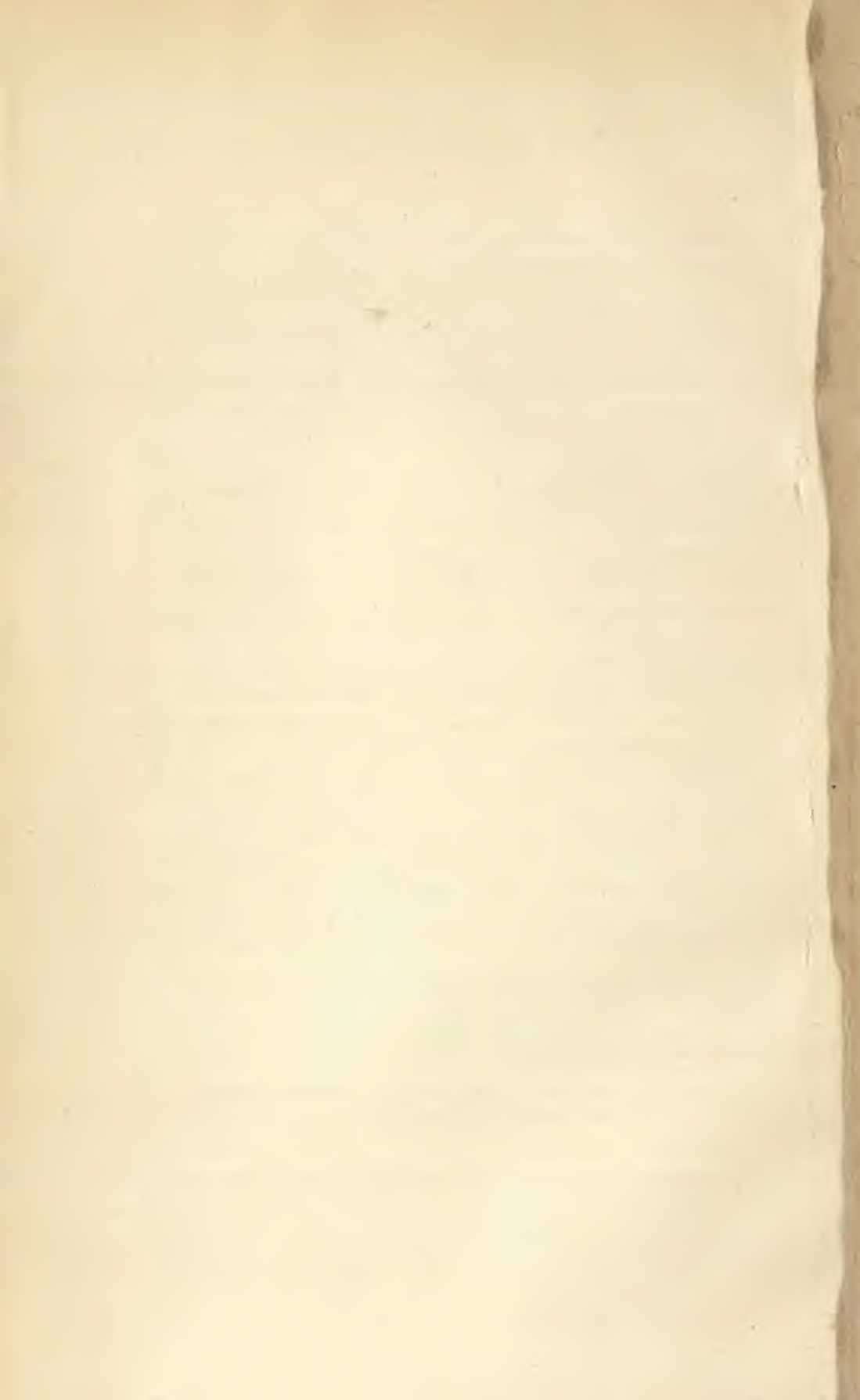
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ABSTRACTS FROM THE MINUTES OF THE MEETINGS

JANUARY TO JULY, 1934

Stated Meeting, January 6, 1934

ROLAND S. MORRIS, LL.B., LL.D., D.C.L., President,
in the Chair.

A letter was read from The Historical Society of Pennsylvania thanking the Society—for presenting to it Volume 3 of "Selections from the correspondence of Honourable James Logan."

The decease was announced of the following members:

Arthur P. Davis, B.S., Sc.D., at Oakland, California,
August 7, 1933, æt. 72.

Alfred F. Hess, M.D., Sc.D., at New York, December 5,
1933, æt. 58.

The following illustrated paper was read:

"A Half-Century of Trituberculy, the Cope-Osborn Theory of Dental Evolution," by William K. Gregory, Ph.D., Professor of Palæontology, Columbia University, which was discussed by Dr. Shaeffer and by Dr. Winsor, a guest.

Stated Meeting, February 2, 1934

ALBA B. JOHNSON, LL.D., Vice-President, in the Chair.

Francis R. Packard, recently elected member, subscribed the Laws and was admitted into the Society.

Invitations were received

from The International Benjamin Franklin Society to be represented at its Annual Meeting and Luncheon on January

20, at the Hotel Plaza, New York City. Russell Duane attended as the delegate of the Society.

from The American Academy of Political and Social Science to be represented at its 34th Annual Meeting at the Bellevue Stratford Hotel, April 7 and 8. Arthur W. Goodspeed and Emery R. Johnson attended as the delegates of the Society.

The following paper was read:

"Time and its Determination," by Ernest W. Brown, Sc.D., Professor of Mathematics, Yale University, which was discussed by Dr. J. A. Miller.

Stated Meeting, March 2, 1934

ROLAND S. MORRIS, LL.B., LL.D., D.C.L., L.H.D., President, in the Chair.

Marshall S. Morgan, recently elected member, subscribed the Laws and was admitted into the Society.

The decease was announced of the following member:

William M. Davis, Sc.D., Ph.D., at Pasadena, California, February 5, 1934, æt. 83.

The following paper was read:

"Conservation and Evolution in a Changing Social Program," by John C. Merriam, which was discussed by Messrs. Sioussat, Leland, Aydelotte, Patterson, E. M., and Emery R. Johnson.

The following resolution was adopted:

RESOLVED: "That the following draft of the Revision of the Laws of the American Philosophical Society in ten chapters, as prepared by the committee on the Revision of the Laws in substitution for the present Laws, be and the same is hereby proposed to the Society at its stated meeting on the 2nd of March, 1934, to be laid before the Society at its next General Meeting in April, 1934, after due notice to the members as provided in the Charter and Laws, for such action as the Society may be pleased to take thereon." The new Laws as proposed follow in the minutes.

General Stated Meeting, April 19, 20, 21, 1934

Thursday Morning, April 19

Business Session, 9:30 o'clock

ROLAND S. MORRIS, LL.B., LL.D., D.C.L., L.H.D., President,
in the Chair.

Burton E. Livingston and Henry A. Sanders, recently elected members, subscribed the Laws and were admitted into the Society.

Invitations were received

from the University of Delaware to be represented at the Celebration of the One Hundredth Anniversary of its Founding to be held May 11-13, 1934, at Newark, Delaware. Charles L. Reese represented the Society.

from the Association Franco-Americaine inviting the Society to participate in the Commemoration of the One Hundredth Anniversary of the death of Lafayette. St. George L. Sioussat acted as a delegate.

from the Edinburgh Geological Society inviting delegates to its Centenary Celebration on September 3, 4, 1934.

The decease was announced of the following members:

Augustus Trowbridge, A.M., Sc.D., Ph.D., at Sicily,
March 14, 1934, æt. 66.

George Owen Squier, Ph.D., Sc.D., at Washington,
March 24, 1934, æt. 65.

Archibald B. Macallum, M.A., M.D., Ph.D., Sc.D.,
LL.D., F.R.S., in Canada, April 5, 1934.

Dr. Waldo G. Leland, the chairman of the committee on "Revision of Laws," presented a copy of the proposed revised laws with also many suggestions of changes received from members. After careful discussion the report of the committee was referred to Council for further consideration.

Opening Session, 10:30 o'clock

PRESIDENT MORRIS in the Chair.

The following papers were read:

- "Cyto-taxonomic Studies on Certain *Oenotheras* from California," by Ralph E. Cleland, Professor of Biology, Goucher College.
- "What Is *Oenothera Hookeri*, Torrey and Gray?" by Bradley M. Davis, Professor of Botany, University of Michigan.
- "New Amplifications of the North American *Piperaceæ*," by William Trelease, Professor Emeritus of Botany, University of Illinois.
- "Some Physico-chemical Properties of the Virus of Typical Tobacco Mosaic," by B. M. Duggar, Professor of Physiological and Economic Botany, University of Wisconsin.
- "New Developments in Automatic Control of Soil Moisture in Plant Cultures," by Burton E. Livingston, Director, Laboratory of Plant Physiology, Johns Hopkins University.
- "The Action of Anæsthetics on Living Protoplasm," by Lewis V. Heilbrunn, Associate Professor of Zoology, University of Pennsylvania. (Introduced by Dr. Calvert.)
- "A New Synthesized Pure-breeding Chromosome Type in the Jimson Weed, *Datura Stramonium*," by A. F. Blakeslee, Assistant Director in Plant Genetics, Carnegie Station for Experimental Evolution, Cold Spring Harbor, A. G. Avery and A. Dorothy Bergner. (Read by title.)
- "Evidence for a Concentrating Neurohumor in the Responses of Fish Melanophores," by G. H. Parker, Director, Zoological Laboratories and Professor of Zoology, Harvard University.
- "The Properties of Catalytic Surfaces as Revealed by Heavy Hydrogen," by Hugh S. Taylor, Professor of Chemistry, Princeton University.

Afternoon Session, 2 o'clock

PRESIDENT MORRIS in the Chair.

Gilbert Chinard, W. H. Collins, W. B. Dinsmore, E. V. Huntington, L. R. Jones, C. A. Kofoed, J. R. Marlin, S. P. Wetherill, recently elected members, subscribed the laws and were admitted into the Society.

The following papers were read:

- "A Spectral Survey of the Nearest Galaxy, the Large Magellanic Cloud," by Annie J. Cannon, Curator, Harvard College Observatory.
- "Molecules in Stellar Atmospheres," by Henry Norris Russell, Professor of Astronomy and Director of the Observatory, Princeton University.
- "Nuclear Physics at the Bartol Research Foundation of the Franklin Institute," by W. F. G. Swann, Director, Bartol Research Foundation.
- "An Apatemyid from the White River Oligocene of South Dakota," by Glenn L. Jepsen, Princeton University. (Introduced by Dr. Sinclair.)
- "Geomorphic Investigations in the Yellowstone Park and Big Horn Regions of Wyoming," by Douglas Johnson, Professor of Physiography, Columbia University.
- "The Report on the White River Fauna," by William B. Scott, Professor Emeritus, Princeton University.
- "New Fishes from the Triassic of Pennsylvania," by W. L. Bryant, Director, Park Museum. (Introduced by Dr. Sinclair.) (Read by title.)
- "Solar Radiation, Lightning, the Azotobacter and Protoplasm," by George Crile, Director, Cleveland Clinic and of the Cleveland Clinic Hospital.
- "Some Illustrative Results with a New Semi-automatic Respiration Calorimeter," by John R. Murlin, Department of Vital Economics, University of Rochester.
- "A simple, Rapid Basal Metabolism Measurement for Hospital Routine," by Francis G. Benedict, Director, Nutrition Laboratory, Carnegie Institution of Washington.

Friday Morning, April 20, 1934

Executive Session, 10 o'clock

PRESIDENT MORRIS in the Chair.

The President delivered his annual report, in which he called the attention of the members to two important steps that the Society has taken during the last year:

1. It has been decided to move the library from its present location to a far safer and more commodious location, viz. to the second floor of the Drexel Building just across fifth Street.

2. From a portion of the income of the Society appropriated for the purpose, the "Committee on Grants," Dr. Conklin, Chairman, has assigned to date (April 1934) a total of about \$40,000 to nineteen applicants deemed especially worthy. These were selected according to certain principles decided upon by the committee.

The Proceedings of the Council were submitted and the nominees were recommended for election.

The Society then proceeded to an Election of officers and members.

The Tellers subsequently reported that the following officers and members had been duly elected:

President

Roland S. Morris

Vice-Presidents

Edwin G. Conklin

Alba B. Johnson

Robert A. Millikan

Secretaries

Arthur W. Goodspeed

John A. Miller

Curator

Albert P. Brubaker

MINUTES

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Councillors

(To serve for three years)

Charles G. Abbot
John Cadwalader
James A. Montgomery
Hugh S. Taylor

Members

Detlev W. Bronk, Wallingford, Pa.
Willa Cather, New York, N. Y.
Gustavus Wynne Cook, Wynnewood, Pa.
Wilbur L. Cross, New Haven, Conn.
Cass Gilbert, New York N. Y.
Edward S. Harkness, New York, N. Y.
Horace Howard Furness Jayne, Wallingford, Pa.
Alfred Vincent Kidder, Andover, Mass.
John-Livingston Lowes, Cambridge, Mass.
Frederick Novy, Ann Arbor, Mich.
Conyers Read, Philadelphia, Pa.
Jesse S. Reeves, Ann Arbor, Mich.
Owen J. Roberts, Washington, D. C.
George Sarton, Cambridge, Mass.
Deems Taylor, New York, N. Y.

Afternoon Session, 2 o'clock

ALBA B. JOHNSON, A.B., LL.D., Vice-President in the Chair.

The following "Symposium on Community Planning" was presented. (The speakers were introduced by Colonel Wetherill.)

"Some Governmental Aspects of Regional Planning," by George L. Radcliffe, First Vice-President and Member of Executive Committee, Fidelity and Deposit Company, Baltimore. Regional Adviser of public works.

"Esthetic Aspects of Regional and City Planning," by Jacques Grèber, Architect, Institut d'Urbanisme.

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"Some of the Economic Implications of National Planning," by Frederick A. Delano, President, American Civic Association and Chairman of the National Planning Board. (Read by Charles J. Rhoads.)

Friday Evening

The R. A. F. Memorial lecture was delivered by Edwin G. Conklin, Professor of Zoology, Princeton University, "A Generation's Progress in the Study of Evolution."

Saturday, April 21

Morning Session, 10 o'clock

EDWIN G. CONKLIN, Ph.D., Sc.D., LL.D., Vice-President in the Chair.

The following papers were read:

- "Linguistic Atlas of the United States," by Hans Kurath, Brown University. (Introduced by Dr. Lingelbach.)
- "The Beatty Papyrus of the Epistles of Paul," by Henry A. Sanders, Professor of Latin, University of Michigan.
- "Recent Archaeological Field Work in Yugoslavia," by Vladimir J. Fewkes, Director, Harvard-American School of Prehistoric Research. (Introduced by Dr. Barton.) (Read by title.)
- "Turkish Remains in Modern Belgrade," by John Dyneley Prince, Professor of Slavonic Languages, Columbia University.
- "The Chalcolithic or Copper-Stone Age in the Near East," by W. F. Albright, Professor of Semitics, Johns Hopkins University.
- "The Long Voyages of the Polynesians," by Roland B. Dixon, Professor of Anthropology, Harvard University. (Read by title.)
- "New Light on Prehistoric Man in Asia," by George Grant MacCurdy, Research Associate in Prehistoric

Archæology and Curator of the Anthropological Collections, Yale University.

"Studies in Human Variation," by Aleš Hrdlička, Curator, Division of Physical Anthropology, U. S. National Museum, Smithsonian Institution.

"Some Aspects of the Constitutional Basis of Pathology," by John W. Gowen, Rockefeller Institute. (Introduced by Dr. Conklin.)

"The Thirty-nine Distinct Lines of Proboscidean Descent and Migration into All Parts of the World Excepting Australia," by Henry Fairfield Osborn, American Museum of Natural History. (Read by Dr. Scott.)

Afternoon Session, 2 o'clock

PRESIDENT MORRIS in the Chair.

The following "Symposium on Problems of Business Recovery" was presented.

"Currency Stabilization," by Ray B. Westerfield, Professor of Political Economy, Yale University. (Introduced by Dr. Johnson.)

"Factors Controlling Prices, Domestic and International," by Ernest M. Patterson, Professor of Economics, Wharton School of Finance and Commerce, University of Pennsylvania.

"Economic Functions of the Stock Market and the National Securities Exchange Act of 1934," by S. S. Huebner, Professor of Insurance and Commerce, Wharton School of Finance and Commerce, University of Pennsylvania.

"Liberty, Property and Recovery," by James T. Young, Professor of Public Administration, University of Pennsylvania.

"Problems of Government Ownership and Operation of Railroads," by Emory R. Johnson, Professor of Trans-

portation and Commerce, Wharton School of Finance and Commerce, University of Pennsylvania.

"Some Subjective Factors Affecting Industrial Recovery," by Samuel Price Wetherill, Engineer.

Saturday Evening

The annual dinner was held at the Bellevue Stratford Hotel. Roland S. Morris presided. The speakers were:

Robert A. Millikan

John Dyneley Prince

PROCEEDINGS
OF THE
AMERICAN PHILOSOPHICAL SOCIETY
HELD AT PHILADELPHIA
FOR PROMOTING USEFUL KNOWLEDGE

VOL. 73 1934 No. 1

THE RATES OF GROWTH, LARVAL DEVELOPMENT AND
SEASONAL DISTRIBUTION OF DRAGONFLIES OF
THE GENUS ANAX (ODONATA: AESHNIDÆ)

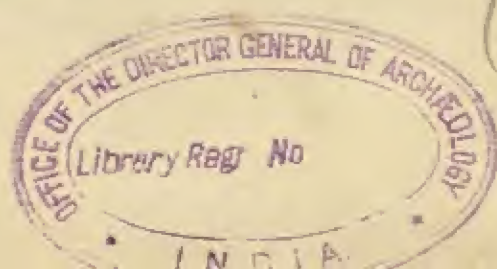
PHILIP P. CALVERT

(Read April 21, 1932)

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IN THE *Proceedings* of this Society for 1929 (volume LXVIII), there appeared a paper on "Different Rates of Growth among Animals with Special Reference to the Odonata," in which I stated that I began the rearing of Odonate larvæ primarily for the purpose of obtaining the morphological differences between the successive larval instars. The



present article deals with morphological and other differentials of the larval instars of some species of the Odonate genus *Anax*.

In the paper of 1929 it was concluded that: The growth factor varies in an irregular way from instar to instar in the Odonate larvæ and in other Arthropoda and these variations are not correlated with changes in the character of the food. It might reasonably be inferred, therefore, that, due to this irregularity, the growth achieved in a given instar by two or more individuals would differ and that in consequence an exact definition of the characters of that instar is impossible. This inference will be found to be supported by that measure by the following observational evidence.

I. RATES OF GROWTH AND IDENTIFICATION OF THE INSTARS OF *ANAX JUNIUS*

The accompanying Table I gives some differences between the successive exuvæ of the one individual of *Anax junius* which has been reared from egg to adult. It is the same individual whose growth curve has been published in fig. 1 of these *Proceedings*, Vol. 68, page 231.

TABLE I

CHARACTERS OF THE LARVAL EXUVIÆ OF A SINGLE MALE OF *ANAX JUNIUS*, REARED FROM EGG TO ADULT (LARVA No. 3)

Exuvie	Inferior Appendages (Cerci) (Ventral View) Mm.	Cercoids, Mm.	Front Margin, Hind Wing Rudiment, Mm.	Antennal Segments	Tarsal Segments	Gonapophyses, Ninth Segment, Mm.	Width of Head, Mm.	Total Length, Mm.
1st	.30	0	0	3	1	0	.73	2.45
2nd	.30	0	0	4	2	0	.9	2.82
3rd	.34	0	0	4	2	0	1.23	3.35
4th	.39	0	0	4	2	0	1.39	3.68
5th	.82	.05	.14	5	2	.03	1.91	7.36
6th	1.06	.11	.22	5	3	.05	2.49	10.14
7th	1.39	.24	.33	5	3	.06	3.03	14.0
8th	1.88	.33	.57	6	3	.08	3.76	18.0
9th	2.62	.57	1.06	7	3	.12	4.62	22.5
10th	3.11	.98	1.72	7	3	.19	5.56	29.5
11th	4.13	1.39	2.74	7	3	.20	6.54	38.
12th	4.99	2.04	5.24	7	3	.33	7.61	44.
13th	5.97	2.86	10.39	7	3	.42	8.5	47.

The exuviae, except the thirteenth, or last, were transferred from the water in which they were shed through 50 per cent alcohol to 70 per cent alcohol. The measurements given in Table I here, except those for the width of the head of exuviae 1-7, were made from the exuviae in alcohol. The width of the head of the first to seventh exuviae was measured after these had been mounted, without compression, in cells in balsam.¹ The data here given for these exuviae are of different values, as will appear from the following considerations. All of these exuviae, with the exception of the last, were shed under water, the last in the air. The water tends to distend the exuviae; the aerial exuvia, especially its abdomen, is more apt to be somewhat shortened, by being telescoped, as the imaginal abdomen is withdrawn from it. The dorsal surface of the head in all the exuviae is split crosswise and also partly lengthwise as described more fully on page 12, to allow the withdrawal of the head of the insect. Although the elasticity of the chitin causes a partial closure of these clefts, enough of an opening may persist, or the edges of the cleft may overlap, to affect the measurement of the width of the head. The total length of an exuvia is the sum total of the lengths of the harder segmental areas (sclerites) of all the somites plus those of the softer intersegmental "sutures." Even in water these latter may not be equally stretched, either at the same moult or at different moults. Measurements of total length from larvae preserved in alcohol are likewise subject to considerable error, as even the use of the same fixative will result in different degrees of extension or contraction of the body in different individuals of the same lot, fixed at the same time. The greater number of possible variables entering into the total body length therefore renders this dimension more uncertain of exact definition than is the case with those parts of the exuviae which consist of but a single segment, such as the inferior abdominal appendages (cerci), superior abdominal appendages (cercoids) and the hind wing rudiment. The lengths of these three organs, therefore, would seem to be

¹ The measurements of the larvae given in the writer's paper of 1929 were made from life, as stated, *loc. cit.* p. 231.

more reliable, as means of recognition of the successive exuviae, so far as size is concerned. Similar reasons have led to the rejection of two other characters which have often been used in previous literature, the points caudad to which the labium (mask) and the wing-rudiments respectively reach. These points are affected by the distension or non-distension of the membranes connecting head, prothorax and mesothorax in the first case and those connecting the anterior abdominal segments in the second.

It will be noticed from Table I that the number of segments of the antennae increases with age and it is conceivable that measurements of the lengths of these segments might furnish additional means of recognition of the respective exuviae. The likelihood of error due to telescoping of these segments, however, appears to be too great to justify reliance on such measurements.

From Table I we may calculate the Brooks, Przibram or Minot growth rates and obtain thereby Table II, which shows that the rate of growth of the parts measured:

- (a) varies from instar to instar,
- (b) is different for different parts in the same instar,
- (c) is higher on the whole in those parts (cercoids, hind wing, gonapophyses) which are to be functional in the adult than in those the significance of which is larval rather than imaginal.

The differences between the rates of growth of the various parts are illustrations of the *heterogonic growth* of Pezard (1918, p. 25) to which Huxley (1932) has directed so much attention recently. On applying the latter's formula, $y = bx^k$, to the data for the wing rudiments, for example, of our Table I, the values obtained for k range from 1.25 to 10.37, and one realizes the truth of his statement concerning Arthropods (p. 68) "that in the life-history of any single specimen the theoretical growth-curve relating organ-size with body-size will never be realized. Instead, growth of both organ and rest-of-body will take place in a series of jumps,

but the points thus arrived at will all lie on the theoretical curve."

TABLE II
GROWTH RATES IN LENGTH OF *ANAX JUNIUS* (LARVA No. 3)

Exuviae	Inf. Appa.	Cercoids	Hind Wing	Gonaps.	Head Width	Total Length
1 to 2	0	0	0	0	1.23	1.16
2 to 3	1.13	0	0	0	1.37	1.18
3 to 4	1.15	0	0	0	1.13	1.10
4 to 5	2.10	0	0	0	1.38	2.00
5 to 6	1.29	2.2	1.57	1.67	1.30	1.38
6 to 7	1.31	2.18	1.50	1.20	1.22	1.38
7 to 8	1.31	1.37	1.73	1.33	1.24	1.29
8 to 9	1.39	1.73	1.86	1.50	1.23	1.25
9 to 10	1.19	1.72	1.62	1.58	1.20	1.31
10 to 11	1.31	1.42	1.60	1.05	1.18	1.29
11 to 12	1.21	1.47	1.91	1.65	1.16	1.16
12 to 13	1.20	1.42	1.98	1.27	1.12	1.07

The "natural logarithmic" percentage rates of growth are slightly lower than those given in this table. (See Calvert, 1929, pp. 253-4 and figs. 4 and 5, pp. 265, 266.)

It is, of course, unfortunate that I did not succeed in rearing more individuals of *A. junius*. I possess 96 exuviae of various ages but mostly of the first and last instars, representing about 93 other individuals, some of them due to the kindness of Prof. A. D. Whedon. I am greatly indebted to Prof. C. H. Kennedy, for the loan of 88 exuviae and 65 larvæ, representing 65 individuals which he had attempted to rear during the summer of 1917 at Ithaca, New York. Of this number, Prof. Kennedy reared one through four successive moults, two through three successive moults, sixteen through two successive moults, as represented by the preserved exuviae and larvæ. The remaining survived only one moult. In transmitting this material, Prof. Kennedy wrote (March 10, 1927):

"I am sending by express the *Anax* reared specimens and the rearing notes.

"On the notes are given numbers of each individual reared starting at No. 100 and running up to No. 170 I believe.

"In the glass vials are corresponding numbers of the specimen

and A, B, C, etc. of the exuviae shed. Larvæ were caught in all stages and reared from the stage A in which caught as far as they lived B, C, D, etc., in hopes that I could patch together later these fragmentary life histories into a complete set of instars. I think I have enough material to give the complete number of instars but have never tried to piece it together. Z is the last instar or adult, I forget which, Y the next to last, X the third from last, etc.

"X, Y, and Z apply only to specimens that emerged into adults.

"The vials have dried out but you are welcome to boil them in KOH or anything to soften them up again."

Prof. Kennedy also sent additional larvæ of *junius* which he had not attempted to rear.

To each vial of Prof. Kennedy's collection whose contents had dried, distilled water was added and allowed to stand for some days. The water was then replaced by 50 per cent alcohol and the latter subsequently by 70 per cent alcohol, in which last the specimens were studied and measured. This treatment seems to have restored them to an approximately natural condition, although it must be kept in mind that a source of error due to the drying and subsequent softening exists. No alkaline hydrate or other substance than distilled water and the alcohols above mentioned has been employed, so that Prof. Kennedy's material might approximate, as nearly as possible the writer's reared material.

The attempt has been made to correlate the exuviae possessed by the writer and those lent by Prof. Kennedy with the exuviae of the reared male ("larva No. 3"). The results of that attempt are set forth in Table III, based on a study of 117 exuviae, with both sexes represented for the later instars at least. An examination of Table III will show that:

1. The range in size of the exuviae of a given moult (e.g., the 8th) is often greater than the difference between the dimensions given for those exuviae and the exuviae immediately preceding and succeeding (e.g., the 7th and the 9th).

2. Some of the dimensions given, especially for the earlier exuviae, overlap those of the preceding or succeeding exuviae. Further, a comparison of Tables I and III shows that:

3. The specimens referred to a given moult in Table III do not in all cases agree with the characters stated for the reared exuvia of the corresponding moult in Table I. Thus, of the eight male specimens referred to the fifth moult in Table III, the three which have preserved their antennæ have but four segments, while the reared male of Table I has five segments. All the specimens (eight males, six females) of the 6th moult, Table III, have two tarsal segments; that of Table I has three. Such disagreements between Tables I and III may therefore well raise the question as to the reliability of Table III and of the methods employed in formulating it. As an example of these methods we may consider the evidence presented by Prof. Kennedy's No. 104. This number is attached to three vials, containing collectively four exuviae and one larva. The data derived from them follow in Table IV:

Assuming that the material was correctly labeled, the identifications, based chiefly upon the lengths of the cerci, cercoids, and hind wing pads, for the reasons given above, seem rational when these four exuviae are viewed as one ontogenetic series. Actual coincidences between the data of Table IV and the corresponding entries in Table I are, indeed, few, being limited to the length of the cercoids and of the hind wing pad in the exuvia of the 5th moult, the number of the tarsal joints in those of the 5th and 7th moults, and the number of antennal joints in those of the 6th and 8th moults. The divergences between the two tables are not in the same ratio for each exuvia.

Another illustration may be taken from Prof. Kennedy's No. 101 (Table V).

Much of the comment on Table IV will apply here also. It is instructive to compare the eighth exuvia of Tables I, IV and V, especially for the hind wing rudiment.

Lastly, Prof. Kennedy's No. 164 supplies the following data (Table VI).

Study of Tables I, IV and VI indicates that in the identification of the growth and developmental stages which are

TABLE III
 RANGE OF CHARACTERS OF LARVAL EXUVIÆ OF ANAX JUNIUS, REARED THROUGH FOUR MOULTS OR FEWER, OR COLLECTED, CORRELATED
 WITH THOSE OF TABLE I

Exuvie	Number of Spins. Studied and Sex	Inferior Appendages (Cerci) (Ventral View) Mm.	Cercoids, Mm.	Front Margin, Hind Wing Rudiment, Mm.	Antennal Segments	Tarsal Segments	Male Gonapophyses, Ninth Segment, Mm.	Female Gonapophyses, Eighth and Ninth Segments, Mm.	Width of Head, Mm.	Total Length, Mm.
1st	6, sex?	.26-.33	0	0	3	1	0	0	.70-.75(.86)	2.37-2.70
2nd	4, sex?	.31-.39	0	0	4	2	0	0	.94-1.14	2.86-3.35
3rd	1♂, 8, sex?	.31-.39	0	0	4	2	0	0	1.00-1.31	3.27-3.44
4th	1♂, 8, sex?	.45-.56	.02	.09	4	2	0	0	1.27-1.64	4.00-5.81
5th	8♂ 2♀	♂ .62-.82 ♀ .62	♂ .02-.05 ♀ .02	♂ .14-.23 ♀ .08	♂ 4 ♀ 4-5	2 2	♂ .03-.05 ♀ .03	8th .03 9th .03	♂ 1.80-2.13 ♀ 1.88-1.96	♂ 6.18-7.53 ♀ 6.30
6th	8♂ 6♀	♂ .98-1.14 ♀ .98-1.23	♂ .08-.14 ♀ .11-.14	♂ .22-.34 ♀ .22-.31	♂ 5 ♀ 5	2 2	♂ .03-.06 ♀ .03	8th .02-.05 9th .02-.06	♂ 2.29-2.78 ♀ 2.45-2.78	♂ 8.67-10.55 ♀ 9.57-10.64
7th	2♂ 1♀	♂ 1.23-1.43 ♀ 1.48	♂ .22-.25 ♀ .20	♂ .37-.44 ♀ .47	♂ 7? ♀ 5	3 3	♂ .03-.06 ♀ .03	8th .08 9th .11	♂ 2.86-3.03 ♀ 2.95	♂ 11.70-14. ♀ 13.09
8th	3♂ 3♀	♂ 1.72-2.29 ♀ 1.72-2.08	♂ .30-.45 ♀ .29-.34	♂ .42-.98 ♀ .56-.74	♂ 6 ♀ 6	♂ 3 ♀ 3	♂ .03-.11 ♀ .03	8th .08-.17 9th .14-.19	♂ 3.35-4.09 ♀ 3.11-4.00	♂ 13.42-19.5 ♀ 15.-17.

TABLE III (Continued)

Exuviae	Number of Specimens Studied and Sex	Inferior Appendages (Cerci) (Ventral View) Mm.	Cereoids, Mm.	Front Margin, Hind Wing Rudiment, Mm.	Antennal Segments	Tarsal Segments	Male Gonapophyses, Ninth Segment, Mm.	Female Gonapophyses, Eighth and Ninth Segments, Mm.	Width of Head, Mm.	Total Length, Mm.
9th	7♂	♂ 2.45-2.78	♂ .50-.72	♂ .98-1.55	♂ 6-7	3	♂ .08-.12	8th .33-.40	♂ 4.09-4.87	♂ 21. -23.
	5♀	♀ 2.21-2.70	♀ .49-.62	♀ .90-1.14	♀ 6	3		9th .26-.36	♀ 4.09-4.91	♀ 16. -24.
10th	5♂	♂ 3.27-3.52	♂ .82-.98	♂ 1.88-2.29	♂ 6-7	3	♂ .14-.19	8th .67-.78	♂ 5.24-5.89	♂ 28.
	3♀	♀ 2.94-3.03	♀ .82-.90	♀ 1.51-1.64		3		9th .48-.62	♀ 4.91-5.56	♀ 29.5
11th	4♂	♂ 3.68-4.66	♂ 1.23-1.51	♂ 2.86-4.58	7	3	.16-.23	8th .98-1.31	♂ 6.38-6.95	♂ 36.5
	3♀	♀ 3.76-4.25	♀ 1.06-1.47	♀ 2.62-3.25	7	3		9th .82-.98	♀ 6.29-6.63	♀ 36. -40.
12th	4♂	♂ 4.50-4.91	♂ 1.64-1.96	♂ 3.93-5.07	7	3	.23-.30	8th 1.55-1.80	♂ 6.55-7.85	♂ 40. -47.
	5♀	♀ 4.83-5.07	♀ 1.64-1.96	♀ 4.17-5.24	7	3		9th 1.31-1.80	♀ 6.54-7.69	♀ 43. -46.
13th	10♂	♂ 5.24-6.30	♂ 2.45-3.03	♂ 8.5 -10.5	♂ 7 ⁴	3	♂ .33-.41	8th 1.96-2.94	♂ 8.0 -9.00	♂ 41.5 -49.
	10♀	♀ 5.32-5.90	♀ 2.33-2.86	♀ 9.0 -11.0	♀ 7-6 ⁵	3		9th 1.88-2.21	♀ 8.5 -9.00	♀ 44. -50.

³ Five in one antenna.

⁴ One of these was the final exuvia (*i.e.*, of transformation to the imago), according to Prof. Kennedy's notes.

⁵ Five in a left antenna ♂ regenerated after injury.

⁶ Six in one antenna only of each of 2 ♀♀.

represented by the exuviae, all available characters are to be taken into account, and that the use of but one feature would often result in error.⁹

TABLE IV

CHARACTERS OF FOUR SUCCESSIVE EXUVIAE OF LARVA NO. 104, *ANAX JUNIUS*, REARED BY PROF. C. H. KENNEDY

Exuvia Probably	Inferior Appendages (Cerci) (Ventral View) Mm.	Cercoids, Mm.	Front Margin, Hind Wing Rudiment, Mm.	Antennal Segments	Tarsal Segments	Male Gonapophyses, Ninth Segment, Mm.	Width of Head, Mm.	Total Length, Mm.
5th	.74	.05	.14	—	2	—	1.96±	6.95±
6th	1.10	.14	.23	5?	2	—	2.70±	9.57±
7th	1.43	.22	.37	—	3	.03	2.86	11.70±
8th	1.72	.30	.42	6	3	.03	3.35	13.42±
larva ⁴	1.88	.41	.65	6	3	.08	3.60	15.00±

TABLE V

CHARACTERS OF THREE SUCCESSIVE EXUVIAE OF LARVA NO. 101, *ANAX JUNIUS*, REARED BY PROF. C. H. KENNEDY

(Same headings for the columns as for Table IV, except *Female* instead of *Male* gonapophyses)

8th	1.72	.29	.69	—	3	8th .11 9th .14	3.11+	15.00±
9th	2.29	.57	.90	—	3	8th .37 9th .36	4.09+	20.00±
10th	2.95	.86	1.64	—	3	8th .78 9th .49	4.91±	24.00±

TABLE VI

CHARACTERS OF THREE SUCCESSIVE EXUVIAE OF LARVA NO. 164, *ANAX JUNIUS*, REARED BY PROF. C. H. KENNEDY

(Same headings for the columns as for Table IV)

9th	2.78	.55	1.23	—	3	.12	4.58	?
10th	3.27	.82	2.13	—	3	.14	5.56+	?
11th	3.68	1.23	4.42	—	3	.17	6.55+	?
larva ⁷	5.32	2.94	9.00	7	3	.20	8.00±	27.00±

⁴ Larva died in rearing, supposedly in the 9th instar.

⁷ Larva died in rearing, supposedly in the 12th instar.

⁸ In fragments.

⁹ Portmann (1921, p. 73) has expressed the same conclusion for the European *Anax imperator*: "Dabei ist zu beachten, dass nur die zusammenfassende Berücksichtigung der verschiedensten Merkmale eine sichere Bestimmung erlaubt, da sowohl die Gliederzahl der Tarsen als die der Antennen in manchen Fällen nicht konstant ist."

The identifications of the exuviae summarized in Table III are based on the data given in Table I, which latter, as already stated, refer to but a single individual. The value of Table I rests solely upon the facts that that single individual was reared from egg to adult, and that the relative rank and age of its successive exuviae are known. No such full information exists for any of the other specimens which I have studied, and as far as I know *A. junius* has not been reared from egg to adult by anyone else. Even in those cases where the later end of an ontogenetic series has been available, the only positive assertion that can be made is that such and such exuviae are ultimate (ult), penultimate (penult), or antepenultimate (tertiult-Calvert 1925), etc. Comparison of some ultimate exuviae (which are aerial, as distinguished from aquatic) with the data of Table I suggests that they are twelfth exuviae rather than thirteenth.¹⁰

There is, moreover, no basis for asserting that "larva No. 3" (Table I) presents the "normal" or "typical" development of its species. Its eminence and its usefulness rest entirely on the chance of its having been reared to maturity.

The exuviae of Arthropods furnish "milestones" in the journey of life, variable though their value may be. Each exuvia marks the end of an instar. A larva may, therefore, be referred to a given instar according as its characters lie between those of two successive exuviae. Larvæ are more frequently encountered in nature than exuviae, so that it is more often desirable to identify the former than the latter. The instar to which a larva of *Anax junius* belongs may, therefore, be approximately determined by finding its place between the columns of Table I, and the data on each instar given in the following sections of this paper have been arranged as a result of this procedure.

¹⁰ Portmann (1921) gives twelve larval instars for a Swiss example of *Anax imperator* which he reared, and the number in other genera of Odonata varies (Balfour-Browne 1909).

II. STRUCTURAL CHANGES IN THE EXTERIOR OF THE
LARVA OF *ANAX JUNIUS*

Egg and Pronymph.—Prof. Kennedy's material contains some eggs embedded within plant tissue and two pronymphs, all dated September 4, 1917. As the contents of these vials also had dried, it seems hardly worth while to give many details concerning them. After having been soaked in distilled water and the alcohols, as above described, the eggs, measured in alcohol, were 1.55 to 1.68 mm. long, .325 mm. in diameter. The contents of each egg had shrunk to 1.39–1.47 mm. in length. The chorion of the anterior or more pointed end of the egg has a reticulated appearance of more or less regular pentagonal and hexagonal meshes, the diagonals of these polygons varying from .0185 to .036 mm. (Pl. II, fig. 26). The chorion of the middle and hind thirds of the eggs lacks this reticulation. The better preserved of the two pronymphs is 2.21 mm. long, and the hindmost fourth of the body is bent ventrad at almost a right angle. The embryonic labium figured by Miss Butler (1904, pl. IV, fig. 2) corresponds to that of the pronymph.

The *larva* of *A. junius* escapes from its exuvia through the following fissures: *a*, a transverse fissure on the dorsal surface of the head; *b*, a mid-dorsal fissure extending from the preceding caudad on to the thorax or even to the abdomen.

The transverse fissure (*a*), of the *first* larval exuvia¹¹ contrary to what occurs in all the following ecdyses, does not extend to either compound eye, its length being equal to only about two-thirds of the distance from eye to eye. It is nearly straight.

The mid-dorsal fissure (*b*) of the *first* larval exuvia has this peculiarity: it extends forward on the mid-dorsal line of the head, apparently as far as the labrum. The two fissures *a* and *b* thus form a cross on the top of the head. This forward extension of *a* is not seen in later exuviae.

Beginning with the second exuvia, the transverse fissure

¹¹ Meaning thereby the exuvia shed at the conclusion of the first larval instar, not that shed at the end of the pronymphal stage.

extends laterad to near the hind margin of each compound eye, thence obliquely forward (latero-cephalad) through the eye and on to its lateral surface (Pl. I, fig. 2). This fissure does not correspond to the frontal sutures of many insects as Snodgrass (1928, pp. 120, 37 and fig. 46 I on p. 121) has pointed out. Whether it is homologous with the postfrontal sutures shown by Crampton for the larval *Chorista* (Mecoptera), *Eremiaphila* (Mantidæ), *Arixenia* and *Anisolabis* (Dermaptera)¹² is a problem for comparative morphology to solve. The area immediately in front of *a* may perhaps still be called *vertex*.

The point at which the transverse fissure (*a*) cuts the lateral margin of the eye, as seen in dorsal view, moves forward (cephalad) during larval development. In the second exuvia the chord subtending the arc posterior to the fissure is to the chord subtending the arc anterior to the fissure as 1 : 2; in the seventh exuvia this ratio is 1 : 1.146; in the tenth 1 : 1.048; in the eleventh 1 : 1; in the twelfth 1 : .87; in the thirteenth (last) 1 : .39. This shifting removes the fissure from the widest part of the head to one of less width.

The transverse fissure (*a*) does not cut the side of the head at the same point in different groups of Odonata. Thus, in the last exuvia of at least some *Æschniinæ*, *Gomphinæ* and *Agrioninæ* (*sensu Selysii*), it cuts through the compound eyes, although not always at the exact point described above for *Anax*; in at least some *Libellulidæ* it cuts through the side of the head anterior to the eyes and in some members of this family (*e.g.*, *Macromia*, *Plathemis*) farther cephalad than in others (*e.g.*, *Libellula*, *Sympetrum*). Thus, Snodgrass's figure (1928, fig. 46 I) represents the moulted skin of a *Libellulid*, not of an *Æschna*, larva.

The mid-dorsal fissure (*b*) extends caudad as far as the hind end of the third abdominal segment in exuviae 1-3, part way into the third abdominal segment in exuviae 4-7, to the hind end of the second segment in exuviae 8-11, to the hind

¹² Crampton 1932, p. 42, pl. VIII, fig. 44; pl. VI, fig. 21; pl. V, figs. 15 and 17 respectively.

end of the first segment in exuvia 12, while in the final exuvia, near the anterior end of the mesothorax, it forks into two fissures, each one running caudad on the lateral margin of the bases of the wing-rudiments as far as the hind margin of the hind wing rudiment, where it stops. The area (tergites) between the wing-rudiments of the opposite sides of the thorax is, therefore, intact in the ultimate exuvia. These fissures of the last exuvia of *Æschna* sp. have recently been described and figured by Henriksen (1932, p. 115 and fig. 8 E).

The anterior part of the *frons* has, in the first instar, about fifteen subparallel striæ on each side of the middle line. Anteriorly most of these striæ are subparallel to the sagittal axis, but posteriorly they curve mesad and approach each other. The most lateral striæ, however, are nowhere parallel or subparallel to the sagittal axis, but are strongly convergent caudad with their fellows of the opposite side (fig. 1, pl. I). Traces of these striæ may be seen in the second, third or even the fourth instar, but not later.

The inner (mesal) margins of the *compound eyes* diverge from each other caudad in the first instar. In the second to the seventh instars inclusive, the inner margins are approximately parallel so that the *frons*, posterior to the antennæ, and the vertex are of almost uniform width. In the eighth instar, the inner margin of each eye at its hind end begins to be prolonged mesad so that the hind margin of the vertex, along the line of the transverse fissure, becomes shorter than the (more anterior) maximum width of this sclerite. This relative reduction increases with each succeeding instar so that in the final exuvia the hind margin is but .42 of the maximum width of the vertex between the eyes. The mesal prolongations of the eyes never meet each other during the larval stage, as they do after transformation. The changes in this and other parts of the body from the last larval instar to the imago are much greater than from the first to the last larval instar.

The number of the corneal facets of the eyes increases with age, as Zimmermann¹² pointed out for larvae of *Æschna*

¹² Zool. Jahrb. Abt. Anat. 37: 9. 1913.

cyanea, as well as the diagonal of the facets. In a first exuvia of *juni*us we counted $182 \pm$ facets on the dorsal surface of one eye, arranged in eighteen or nineteen rows parallel with the anterior and posterior margins. On the ventral surface the arrangement is more complicated and the number of facets possibly greater. The dorsal surface of each eye has more than 200 facets in the second instar, and more than 300 in the third. No attempt has been made to determine their number in later instars. The diagonal of one facet in the posterior dorsal part of an eye was .013 mm. in the first exuvia, .0325 mm. in the eighth, .052 mm. in the 13th (last) exuvia, and .065 mm. in the imago of the same individual (No. 3).

The increase in the number of *antennal segments* from three in the first instar to seven in the last is set forth in Tables I and III (pages 2, 8-9). Table VII shows the growth

TABLE VII

LENGTH IN MILLIMETERS OF THE SEGMENTS OF THE ANTENNAE IN THE SUCCESSIVE EXUVIAE OF *ANAX JUNIUS*, LARVA No. 3

Exuvia	Seg. 1	Seg. 2	Seg. 3	Seg. 4	Seg. 5	Seg. 6	Seg. 7
1	.01	.06	.21				
2	.01	.06	.07	.17			
3	.03	.06	.08?	.12?			
4	.03	.08	.11	.19			
5	.04	.09	.10	.08	.26		
6	.08	.09	.13	.10	.26		
7	.10	.14	.19	.12	.28		
8	.11	.16	.14	.09	.16?	.34?	
9	.16	.16	.23	.14	.19	.22	.23
10	.20	.22	.34	.17	.25	.26	.28
11	.23	.28	.48	.20	.31	.31	.32
12	.31	.36	.73	.25	.34	.34	.31
13	.33	.39	.98	.30	.41	.41	.39

The measurements in the above table which are followed by a question mark were made from the exuviae floating in alcohol from segments which later became detached and lost before the results were checked by remeasurements. They are therefore not as reliable as the others.

of the antennal segments in the successive exuviae of larva No. 3, but the caution indicated on page 4 should be ob-

served in applying these figures to other individuals. As long as the number of segments is not more than six, the distal segment is the longest; when seven segments are attained the third segment is as long as (ninth instar), or longer than (tenth and following instars), any other segment. The measurements given indicate that the third segment is the growing point and gives rise by division to the third and fourth segments when the increase in number from three to four, four to five and five to six occurs, but that the increase from six to seven results from a division of the sixth, or most distal segment.

Changes in the *labium* (mask) are exhibited in the distal margin of the mentum (median labial lobe) and in the labial palps (lateral lobes). Those of the distal margin of the mentum are shown in figs. 6-14, pl. I, which obviate a detailed description. Most of these figures show two median clefts of this margin, a shallower, distal, open cleft and a deeper, proximal closed cleft (figs. 8-13). The latter alone is visible in our fig. 6 of the first exuvia and appears to be the same as that shown by Miss Butler (1904 in her fig. 3, pl. IV); it extends proximad to beyond the level of the chord subtending the arc of the median mental lobe and would appear to be reminiscent of the fusion of the right and left second maxillæ to form the labium. It may be termed the *primary ligular cleft* or *fissure* (PF). In the second exuvia (our fig. 7) it has closed by the fusion, or deposition, of chitin between its opposing margins. It persists as a closed fissure in all subsequent larval exuviae of this and all other species of *Anax* studied and in all of them reaches proximad to beyond the level of the chord mentioned. The other, distal cleft, very shallow in the second exuvia (fig. 7), becomes deeper in each successive exuvia, but in *junius* never attains the level of the chord (figs. 8-13). This cleft has, therefore, nothing to do with the fusion of the right and left second maxillæ into the labium and may be designated as the *secondary ligular cleft* or *fissure* (SF). Microscopic slides of labia of larvæ about to moult (9th and 10th instars) show that the new

median mental margin, which is being withdrawn from the corresponding cuticle, is cleft proximad to enclose the primary ligular fissure (pl. I, fig. 12 R).

Our figs. 8-14 also show the presence of a pair of paramedian mental teeth differentiated from the others from the third instar on and persisting to the time of transformation. Prof. C. F. Byers (1927, pp. 66, 68) having stated that there are no teeth on the distal border of the mentum in *junius*, a lot of 23 male, 19 female last exuviae, all collected at Smithsonian's pond, Cheyney, Pennsylvania, August 12, 1932, within a length of 10 meters, were examined under a 10 mm. objective (Zeiss A) with the following results which were sent, with some of the specimens, to him: No paramedian mental teeth 1 ♂ 1 ♀, vestiges of such teeth 1 ♀, a tooth on one side only 1 ♂, a tooth on both sides 19 ♂ 15 ♀, one tooth on one side, two on other side 2 ♂ 1 ♀, two teeth on each side 1 ♀.

He replied (Feb. 4, 1933): "I looked over the specimens and checked them with my collection of similar material. Of a series of exuviae taken at one pond on one date, I found the following: 10 ♂ without teeth on the distal border of the mentum, 4 ♀ without teeth, 3 ♂ with, one of which had one on one side only, 0 with two teeth to a side. The material from which I wrote the paper was entirely lacking in teeth. Some Michigan material had the teeth, etc. Also a series of specimens of late nymphs (not exuviae) of what I think to be *Anax longipes* also showed this variability in mental teeth. You are quite correct, I feel, in disregarding the mental teeth as taxonomic characters." It is also of interest to note that the distal mental margin, by the acquirement of slender setae or hairs, .018-.025 mm. long, in the fourth and fifth instars, reaches a condition which persists without change, except in the increased number of these hairs, to the time of transformation.

Changes in the labial palp involve both the outlines of the organ and the appearance of setae. The shape of the labial palp in the odd-numbered instars is given in our fig. 27, pl. II, wherein it will be seen that after the fifth instar the

outer distal angle of the "fixed hook," below which the figures "7," "9," "11" and "13" have been placed, becomes more and more rounded off while the inner distal angle becomes more produced and pointed. These changes are a specific character of *Anax junius*, for in other species of the genus (e.g. *amazili*, *longipes* and, to a smaller extent, *imperator*), the truncated character shown in the earlier instars of *junius* is preserved until metamorphosis. The denticles or crenulations along the (morphologically) inner or mesal margin of the labial palp shown in our figs. 27, 28, increase in number from about five in the first instar to fifteen in the sixth and twenty-three in the last. There are also feeble crenulations on the distal margin of the "fixed hook" which are not shown in our fig. 27. These number about eleven in the first six or seven instars (fig. 28), then decrease to six or fewer in the twelfth and thirteenth. The "produced and pointed" inner distal angle, to which reference was made above, is, in the first instar, but slightly longer, or no longer, than the adjoining denticles or crenulations of the mesal and distal margins.

The proximal segment of the labial palp has, in the first instar (fig. 28), on its dorsal surface, near the outer (lateral) margin and near the base of the distal segment (movable hook), one seta .016-.018 mm. long. In the second instar a second dorsal seta is added, also near the base of the distal segment, but more distant therefrom and from the outer margin than is the first seta. These two dorsal setæ persist until the fifth instar, when the first one disappears but one or more setæ may be added near the second seta in a line extending toward the base of the segment. In the last two (twelfth and thirteenth) larval instars there are 7-8 dorsal setæ on this segment in one or more irregular rows extending from near the base of the distal segment proximad.

Ventral setæ are also present on the proximal segment of the palp but are shorter (.012-.02 mm.) and more slender. They number three or four in the first instar and are located: One at .11-.22 of the length of the segment from the base and

near the external margin, one at .50 to .64 of the length and near mid-width of the segment, one at .87-.94 of the length, also near mid-width, and one near the base of the distal segment; this fourth seta does not seem to be always present. These three or four setæ are visible in the second instar, when one or two additional setæ may appear and their numbers increase with each subsequent instar. The distal segment (movable hook) possesses no setæ on its dorsal surface in the first instar, one seta at one-third to one-fourth of the segment's length in the second instar, often two in the third instar, two to three in the fourth instar, three to four in a row in the fifth instar, and about forty in the last instar; these setæ are very short in comparison with the width of the movable hook itself.

Miss Butler (1904) has described and figured two embryonic and two larval stages of the labium of *A. junius*. Her figs. 3 and 4 (pl. IV) represent dorsal views in the first and second larval instars respectively, except that I have found only one, instead of two, dorsal setæ in the first instar.

As the labium of *junius*, with more or less of the head to which it is attached, is not infrequently found floating in the waters where this larva lives, it may be useful to give the maximum length and width of the mentum in each of the thirteen exuviae of reared larva No. 3. They are as follows (in millimeters):

1 .42, .37	4 .86, .62	7 2.37, 1.59	10 4.83, 3.11
2 .53, .44	5 1.39, 1.02	8 3.03, 2.00	11 5.97, 3.72
3 .67, .53	6 1.80, 1.25	9 3.93, 2.53	12 7.44, 4.74
	13 8.59, 5.81		

The Brooks growth-rate was calculated from these dimensions, with the result that in most cases the growth-rate for width was different from that for length, even at the same time, and both were different from those given in Table II, page 5.

The *supra-coxal processes* (legbase processes, supracoxal armature) of the prothorax are the lower or ventral ends of the proepisternum and proepimeron respectively. In early

larval instars no interval or notch is between them, but it becomes apparent in the fourth instar of some larvæ and is more marked with each following moult.

In the fourth or fifth instar, in which the wing rudiments first appear, differentiation of the *meso- and metathoracic pleura* begins. A dark line (suture) runs ventrad and slightly caudad from each ridge constituting the first rudiment of the wing to the base of the coxa, thus separating the episternum from the epimeron. The infraepisterna (katepisterna) become more clearly delimited than the adjacent parts, just as they are in the last larval instar. At this period the right and left mesopleura are widely separated from each other dorsally, but, as is well known, they reach farther and farther dorsad, anterior to the front wing rudiments, with each successive instar. In the thirteenth instar they almost touch along the mid-dorsal line. Between them lies a longitudinal fold or ridge, .24 mm. wide at most; whether this is a vestige of the mesonotum or not is a question requiring perhaps a histological examination for answer. The *wing-rudiments* which in the fifth and sixth instars have the future costal margin, identifiable by the darker chitin, facing caudad, have that same margin facing mesad and caudad in the seventh and mesad and dorsad in the following instars to the time of transformation (Comstock & Needham 1898-99, p. 847).

The increase in the number of *tarsal segments* is displayed in Tables I (page 2) and III (pages 8-9). Divided setæ are present on all the tibiæ in the first and all following instars, on the tarsi of at least some individuals of the first instar, and probably on all tarsi in later instars.

Of the processes which terminate the abdomen, the cerci (inferiors) and the cercoids (laterals) are included in Tables I and III. Each *cercus* in the first instar has a terminal seta .16 mm. long, as well as other setæ, all of which are easily detached in preserved material; excluding the seta the cercus is longer than, or subequal to, the combined lengths of the sternites of segments 9 and 10. In the second instar the terminal seta is .08 mm. long. The *mid-dorsal process*, in

the first instar, is much wider at base (.12-.14 mm.) than long (.08-.10 mm.), abruptly narrowed at two-third's length, and the apex is roundly pointed. In the second instar the apex is truncate and distinctly, barely, or not, excised; from the fourth instar on the apex is distinctly bifid. In the sixth instar the process reaches a length which is greater than half the length of the cerci and which exceeds its own width at base, and retains these relations throughout the remaining larval life. A faint indication of the formation of the inferior appendage of the male imago appears in the tenth exuvia, where the slightly bilobed apex may be seen within the mid-dorsal process at about one-sixth of its length. It is in the same exuvia that the first traces of the copulatory apparatus appear on the ventral surfaces of segments 2 and 3. The gonopophyses of the ninth segment appear much earlier, as is shown in Tables I and III.

The interest attached to these different dates of appearance ontogenetically is obvious. The Odonata share with other insects the site of the exit of the ejaculatory duct on or near the ninth abdominal segment. The copulatory apparatus of the second and third segments of the imago, although said to date at least from the Jurassic (Hagen 1866, p. 5, Taf. II, fig. 1; Backhof 1910, p. 700), is a peculiarity of the Odonata alone.

The surface of the *cuticle* in the first instar is thickly studded with minute denticles (.003 mm. and less in length), which are larger on head (pl. I, fig. 1) and thorax but decrease in size on the abdomen. On the tergites of the thoracic and first four abdominal segments they tend to be arranged in transverse lines and the same is true, to a slighter degree, on all the abdominal sternites. I have not been able to find them in the scanty pronymphal material above mentioned. In the second instar these denticles are fewer and less pronounced. From the third and following exuviae they disappear.

The hind angles of the head are, in the final exuvia, studded with about 100 dark colored teeth, arranged in dorso-

ventral rows, more numerous on the ventral than on the dorsal surface. Each tooth forms an inclined ridge whose length may be as much as .08 mm., but most of them are smaller than this. I have traced these teeth back to a small number visible in the fourth exuvia but have not been able to connect them with the minute cuticular denticles described in the preceding paragraph.

In the sixth instar, when the lateral scars (see page 26) have made their appearance, a transverse row of denticles pointing caudad is present on the dorsal surface of abdominal segments 1-10 and, less marked, on the ventral surfaces of 6 or 7-9. These rows are on the posterior half of each segment, but are nearer to the hind margin of some than of others. On 6-9 they run to the base of the corresponding lateral spine or the homologue thereof. Opposite each lateral scar the dorsal row of denticles is interrupted (text fig. A). These dorsal rows, with these interruptions, are present in all following instars up to transformation. By the ninth instar the transverse ventral rows also, with corresponding interruptions, are present on all the abdominal segments and likewise remain until metamorphosis. Similar dorsal rows of denticles are to be found on the thoracic segments where they do not extend so far laterad (pl. I, fig. 5).

Chatotaxy.—Setæ are present on the body and in early instars are distinctly bilaterally symmetrical, as long ago stated (Calvert 1895) for the youngest larvæ of other species of Odonata. In the first instar most of them are very short (.024 mm. or less) and slender and difficult to see except on exuviae. The pores on which they are located are more easily seen as white disks ($.003 \pm$ mm.) on the brown chitin. The setæ are paired, of course, but only those of one-half of each area are listed.

The dorsal setæ are as follows: Cephalic (Pl. I, fig. 1): 2 or 3 postantennal among the anterior parts of the frontal striæ; 1 anterior vertical; 1 posterior vertical near the hind margin of the head; 2 postocular near the hind angle of each eye and 1-3 postgenal behind the postocular. Thoracic: On

each segment, in at least some individuals, 1 paramedian; 1 dorso-lateral; 2-3 antero-lateral. Abdominal: 1st and 2d segments, 1-3 dorso-lateral; 3d segment, 1 paramedian, 1-3 dorso-lateral; 4th segment, 1 paramedian, 4-6 dorso-lateral; 5th-7th segments, 1-2 paramedian, 3-9 dorso-lateral, 1-6 lateral; 8th and 9th segments, 1 or 2 paramedian, 3-7 dorso-lateral, 1-4 lateral; 10th segment, 1 paramedian, 3-7 dorso-lateral. On segments 5-9 the paramedian pair is distinctly anterior to the dorso-laterals, which are arranged in a wavy, transverse line. On segments 3, 4 and 10, the paramedians are almost on the same level as the dorso-laterals. When there are two paramedians one is anterior, the other posterior behind the corresponding anterior.

The ventral setæ are: Cephalic: 3 infra-genal, in a roughly transverse row. Thoracic: On each of the three segments, 1 latero-sternal very long (.058-.086 mm.), much longer and stouter than any other setæ on the entire body except on the legs and caudal appendages.

Abdominal: 1st segment, 1 sternal; 2d and 3d segments each, 1 antero-sternal, 1 postero-sternal; 4th segment, 1 antero-sternal, 1-2 intermedio-sternal, 1 postero-sternal; 5th-8th segments each, 1-2 antero-sternals, 2-3 intermedio-sternals, 1-2 postero-sternals; 3d to 8th segments may have in addition 1-2 latero-sternals; 9th segment, 2 antero-sternal, 1-2 intermedio-sternal, 1-4 postero-sternal; 10th segment, 1 antero-sternal or 3-4 sternal.

The number and arrangement of dorsal and ventral setæ on the abdominal segments, while bilaterally symmetrical for a given segment, is often different in two successive segments and it is not always possible to classify them into definite groups as is done in the preceding list.

In the second instar, dorsal setæ are as follows: (in some) a median frontal (Pl. I, fig. 2), 5-6 postantennals, 2 anterior verticals, 2 posterior verticals, 6 postoculars, 3 or 4 postgenals, with some additions to the thoracic and abdominal numbers.

The numbers and length of the setæ increase with succeeding instars and it becomes impossible to recognize the

bilateral symmetry. In the last instar they are very numerous and vary from .10 to .28 mm. in length on the abdomen.

III. COLOR CHANGES IN THE LARVA OF *ANAX JUNIUS*

The *first instar* has the body brown (pale fuscous), with the following whitish: A dorsal cross on the head, its anterior arm widest, its posterior arm longest, the intersegmental articulations throughout, a mid-dorsal longitudinal spot or band on the entire length of abdominal segment 8 and, in some, such a band from the prothorax to the second abdominal segment inclusive. The eyes are the darkest part of the body—a purplish-black—as throughout larval life.¹⁴ A figure of this instar has been published by Prof. Needham (1898, p. 67, fig. 71 A; Needham & Betten, 1901, p. 471, fig. 14 A).

In the *second instar* the body is generally brown, most of the intersegmental articulations, first, second, anterior part of third and all of the eighth abdominal segments are much paler or white,¹⁵ thus giving a "belted" appearance to the larvæ which may persist into the ninth instar but not later. In some individuals the metathorax is as pale as the first abdominal, the mesothorax almost as pale, the ninth and tenth abdominal yellow. One exuvia (Kennedy's No. 141) which I refer here shows no belting; the succeeding larva, however, is belted. The markings on the head are apparently not constant; some have, others have not, the white cross of the first instar.

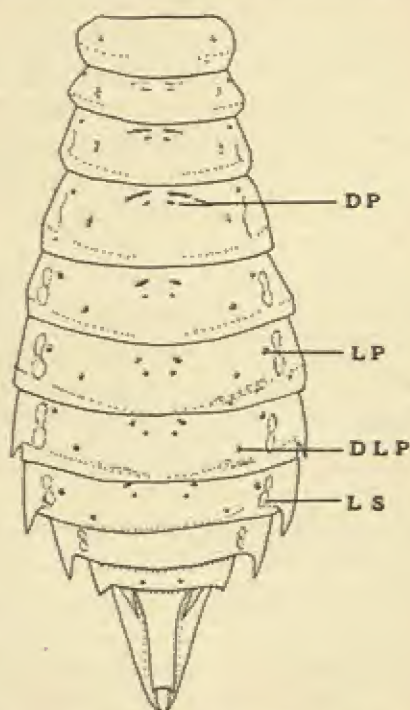
In the *third instar* the body is brown with the following markings pale: Those on the dorsal surface of head variable, a median spot, approximately in line with the bases of the antennæ (= part of the anterior arm of the cross of the first instar), a transverse stripe between the eyes but not reaching

¹⁴ The eyes of the exuviae are colorless.

¹⁵ The parts described for the different instars as "pale" or "white" are in life white, pale cream-colored, or pale green. So also the brown, or dark markings generally, are olive, olive brown, or "cologne earth." The last is illustrated in the color plate of J. B. Smith's *Explanation of Terms Used in Entomology* (1906), but what is described in the present paper as "pale green" is very much paler than the color so labeled on Smith's plate.

them (except as a fine line bordering the lateral arms of the transverse (*a*) suture anteriorly), sometimes interrupted mid-dorsally (= the two lateral arms of the cross of the first instar), and in some a line, widening caudad (= posterior arm of the same cross) and a narrow oblique stripe running from the hind margin of each eye caudad and mesad. The "belted" coloration of the trunk of the second instar is retained in its general features, with the same variations as mentioned thereunder.

The third exuvia of larva No. 3 (the one reared from egg to imago), now mounted in balsam, shows the belted coloration of the abdomen, but some exuviae included as third in our Table III and some larvæ from Prof. Kennedy, which appear to be of this instar, now preserved in alcohol, do not show it.



TEXT FIGURE A.—*Anax junius* Drury, Antigua, probably ninth instar. Abdominal color pattern. From Calvert 1928.

DLP dorso-lateral punctum, DP dorsal puncta, LP lateral punctum, LS lateral scar.

In the *fourth instar* pale markings on the brown body are visible on the dorsal surface as follows: A median anterior (but not cross-shaped) and, on each side a postantennal spot, also the dorsal cephalic sutures, a mid-dorsal line on the pro- and meso-nota (or the whole mesonotum), the whole of the metanotum and of abdominal segments 1-2 or 1-3 and usually 8, hind margins of 4-7 and 9. On the ventral surface the metasternum, the first three and the eighth abdominal segments, as well as the hind margins of 4-7 and of 9, are pale.

In the *fifth instar*, a pale anterior postantennal spot appears on each side of the head raising the total number on the dorsal surface to five. The pale median anterior spot is cross-shaped in some; in some there is also a pale median spot anterior to it. It is usually in this instar that darker brown dots and short lines appear on the abdomen which have been noted by most writers on *Æshnine* larvæ. They correspond to the dorsal points of attachment of certain larval muscles. The names applied to these spots by different authors and the muscles corresponding to each spot are given in Table VIII, in the compiling of which I have had the kind assistance of Professors Walker and Whedon.

TABLE VIII
DORSAL ABDOMINAL MARKINGS AND MUSCLE ATTACHMENTS

Names of Tergal Surface Markings on Abdomen of <i>Æshnine</i> Larvæ			Corresponding Origin of Larval Muscles
Cabot, 1881, p. 23, pl. II, fig. 2	Walker, 1912, pp. 13-14, pls. 6 and 7	Calvert, 1928, pp. 13-14, pl. II, fig. 18	Whedon, 1919, p. 406, pl. XXIII, fig. 11
Dorsal spots (four)	Dorsal puncta (2 pairs)	Paramedian marks (four)	(anterior pair) tertiary longitudinal tergals (posterior pair) quaternary longitudinal tergals
Lateral spots (four)	<div> <div>Dorso-lateral puncta</div> <div>Lateral puncta</div> </div>	<div> <div>Inner-posterior spot</div> <div>Outer-anterior spot</div> </div>	<div> <div>Sextic longitudinal tergal</div> <div>Quinary longitudinal tergal</div> </div>
Polished impressions (two)	Lateral scar	8-shaped mark	Dorso-ventral segmental

Not all of these tergal markings appear at once. Adopting Prof. Walker's terms, the eight more central markings, viz.: The four dorsal, the two dorso-lateral and the two lateral puncta, of abdominal segments 4-7 are the first-comers. A little later these are visible on segment 3 and about the same time the lateral scars on 4-7. Among Prof. Kennedy's material are two larvæ which I refer here but which do not show the "belted" coloration.

In larvæ of the *sixth instar* I have noted a small pale spot behind each eye and the dark brown tergal markings on abdominal segment 8 as additions. In at least one larva the mesothorax was white, like the metathorax. The first three and the eighth abdominal segments usually retain their pale background, but among Prof. Kennedy's larvæ are three which seem to lack these belts.

Seventh Instar (Pl. III, fig. 40).—Labrum, clypeus and frons anterior to the antennæ pale, remainder of the dorsum of the head brown with the following pale spots: The median anterior cross-shaped, its anterior arm longest and reaching to the pale of the frons, a small spot (absent in some) on each side of this arm, the anterior and the posterior postantennal spots (these two confluent in some) and five spots posterior to the transverse moulting fissure, viz.: One mid-dorsal (absent in some), and two on each side, the more lateral of the two wider and behind the eye.

A paramedian brown stripe on each side of the mid-dorsal line on meso- and metanota, but not extending as far laterad as the wing-rudiments.

Abdominal segments 1 and 3 with an ill-defined brownish area on each side of the mid-dorsal line, 2 uncolored, 3 with the dorsal puncta similar to, but not as dark as, those on 4-7, the anterior pair on the anterior edge of the ill-defined brownish areas, the posterior pair on the inner (mesal) edges of the same. The remainder of the abdomen is as described for the sixth instar. Prof. Needham's figure (1898, p. 67, fig. 71 B; Needham & Betten, 1901, p. 471, fig. 14 B) of a nymph one-fourth grown is probably of the sixth or seventh

instar. Four larvæ among fourteen of this instar received from Prof. Kennedy are not belted.

Eighth Instar (Pl. III, figs. 41-42).—Head similar to that of the preceding instar; in some a pale curved longitudinal stripe laterad to the two postantennal spots.

A mid-dorsal longitudinal brown band on the nota of all three thoracic segments, or on the first two only (divided by a pale mid-dorsal longitudinal line), whose width is greatest on the pronotum and on meso- and metanota may or may not reach laterad to the wing-rudiments; an oblique brown streak or spot immediately anterior to the front or to both wing rudiments; a lateral longitudinal brown stripe on the first two or all three segments and the cervical process, ventral to the wing-rudiments and dorsal to the leg-bases.

There is considerable variation in the coloring of the abdomen of the larvæ referred to this instar. Segments 1, 2 and 8, with the metathorax, may be pale with none of the tergal muscle markings (fig. 42), or they may be brown with these markings as in 3-7 (fig. 41); 3-7 have a pale interrupted mid-dorsal longitudinal line which is expanded within the dorsal puncta of each segment. Lateral scars appear on 9 and one pair of dorsal puncta on 10. Short oblique pale streaks confined to one segment make, with similar streaks on adjoining segments, zigzag longitudinal stripes as shown in our fig. 41, pl. III.

Of seventeen larvæ from my own and four from Prof. Kennedy's collection, all of the latter four lack, the seventeen possess, the pale belts.

Ninth Instar (Pl. III, fig. 43).—The larvæ are similar to and show the same variations as those of the eighth instar. In one larva the small pale spot on each side of the anterior arm of the pale median anterior cross-shaped spot on the frons is fused with that arm; the arm itself does not always reach forward to the pale preantennal area of the frons.

A larva of the ninth instar, from Antigua, B. W. I., has been described and figured by Calvert (1928, p. 12, pl. II, figs. 15, 17, 18).

Tenth Instar (Pl. III, fig. 44).—Pale brown invades the whitish preantennal area of the frons and the basal part of the clypeus. A brownish spot shows on meso- and meta-pleura (larger on the latter), ventral to the lateral brown stripe, but a short distance above their respective legs. There are now five longitudinal brown stripes for the whole length of the abdomen: 1. the mid-dorsal, continued from the thorax and divided lengthwise by the pale median line, already described for the eighth instar, but on 1-9 interrupted by still darker brown at the intersegmental articulations; 2. a dorso-lateral on each side from 1-10 enclosing the dorso-lateral puncta; 3. a lateral on each side, continuing the lateral brown stripe of the thorax and enclosing the lateral puncta. On segments 1-4 these five are separated by the oblique pale stripes mentioned under the eighth instar, but on 5-10 these separating pale stripes are shorter, causing the brown stripes to become more or less confluent. Below the lateral scars (and their homologues on 1 and 10) the margins of 1-10 are brownish. The white-"belted" coloration has disappeared from the abdomens of all larvæ referred to this or later instars. Prof. Needham's figure (1898, p. 67, fig. 71 C; Needham & Betten, 1901, p. 471, fig. 14 C) of a nymph "one-half grown" is probably referable to the tenth instar.

From the tenth instar on the coloration pattern appears to change but little (Pl. III, figs. 45, 46).

It will be noted that in describing the coloration of the second to ninth instars inclusive, in which most individuals show the pale-belted condition, mention has been made of other examples in which the pale bands are missing. Whether this is a genetic difference between strains of larvæ, or has some other significance, can, perhaps, only be determined by breeding and rearing experiments on a large scale.

Portmann (1921, p. 73) has made similar observations on the European *Anax imperator*: "Ebenso ist die Zeichnung bald dunkler, oft fast schwarz, und bald heller." Tillyard (1916, p. 69) remarks of the Australian *Anax papuensis*: "Curiously enough, very young larvæ are quite differently

coloured, being either nearly black or black with broad white bands running transversely, or, in fact, in any stage of piebaldness: some may be dull brown very much like young larvæ of *Æschna brevistyla*. Piebald larvæ are seldom found more than 12 mm. long."

IV. SUMMARY BY INSTARS OF THE STRUCTURAL AND COLOR CHANGES OF THE LARVA OF *ANAX JUNIUS*

It will be well to sum up here, by instars, the changes in the various parts of the body which have been described in the preceding pages. The following summary, *together with Tables I and III*, will serve as a means of identifying the several instars. See also page II.

First Instar.—Subparallel striæ on the frons, three antennal segments, the characteristic teeth on the distal mental margin (Pl. I, fig. 6); one dorsal seta on the proximal segment, none on the movable hook, of the labial palp; one tarsal segment; apex of mid-dorsal abdominal process roundly pointed; minute cuticular denticles over the body; a pale dorsal cross on the head, a pale mid-dorsal spot or band on abdominal segment 8.

Second Instar.—Four antennal segments, the characteristic teeth on the distal mental margin (Pl. I, fig. 7); two dorsal setæ on the proximal segment, one on the distal segment of the labial palp; tarsal segments increased to two; pale "belts" usually present on the first two and the eighth abdominal segments and remain until the tenth instar.

Third Instar.—The teeth on the distal mental margin are characteristic (Pl. I, fig. 8); the minute cuticular denticles have disappeared; the pale mid-dorsal cross on the head of the first instar is modified from now on.

Fourth Instar.—The teeth on the distal mental margin are characteristic, fine setæ begin to appear on the distal mental margin in addition to the teeth (Pl. I, fig. 9); the notch between the prothoracic supra-coxal processes begins to appear; the wing rudiments begin to show in this or the following instar, together with differentiation of the meso-

and meta-thoracic pleura; apex of mid-dorsal abdominal appendage distinctly bifid; denticles begin on the hind angles of the head.

Fifth Instar.—The antennal segments increase to five in this or the following instar; first trace of the gonapophyses on eighth and ninth abdominal segments (♀), or ninth only (♂); tergal muscle markings appear on the abdomen.

Sixth Instar.—The outer distal angle of the end or fixed hook of the labial palp begins to be rounded off (Pl. II, fig. 27); tarsal segments increase to three in this or the following instar; mid-dorsal abdominal appendage longer than half the length of the cerci and longer than its own width at base; transverse dorsal anteapical row of denticles appears on each abdominal segment.

Seventh Instar.—The anterior margins of the wing rudiments now face mesad instead of laterad (Pl. I, fig. 4).

Eighth Instar.—Inner margin of each eye at its hind end begins to be prolonged mesad, antennal segments increase to six.

Ninth Instar.—Antennal segments increase to seven in this or the following instar.

Tenth Instar.—Inferior appendage of male imago ("male prominence") begins to show within the mid-dorsal abdominal process, first trace of copulatory apparatus on second and third abdominal segments of the male; no pale "belts" on the abdomen.

Differentiation of the *eleventh and following instars* is apparently only possible from the dimensions given in Tables I and III.

It is of interest to compare the preceding summary for *A. junius* with that given by Portmann (1921, pp. 73-74 and Tafel I) for *A. imperator* of Europe, the only other species of this genus recorded in the literature as having been reared from egg to imago. The differences between the two summaries are as follows:

Portmann gives no change in the number of antennal and tarsal segments in the second "stadium" [instar] from those

in the first, but states that this increase occurs in the third stadium;¹⁶ he finds that the markings of the head of the second stadium are constant, whereas in our *junius* they vary. The increase in length of the wing rudiments from the seventh stadium on he expresses by noting the points on the thoracic or abdominal segments which they reach, while I have preferred to give their absolute lengths in millimeters for the reason given *antea*, page 4. He lists only 12 larval stadia as against thirteen for *junius* but as already stated (*antea*, page 9, Table III, footnote), one *junius* of Prof. Kennedy's collection emerged from an exuvia corresponding to the twelfth of our reared male. Otherwise his and our results for the two species agree very well.

V. THE LARVAL INSTARS OF *ANAX AMAZILI*

In 1909-10, we reared some individuals of *Anax amazili* at Cartago, Costa Rica. Three of these, Nos. 25, 40, 41, were of the last larval instar when collected, as on moulting they yielded imagos between August 31 and September 10, 1909, between December 7 and 10, and on December 25 respectively, all males; their exuviae were preserved. Larva No. 32, after moulting four times, died between January 16 and 29, 1910; its dimensions fall between those of its last exuvia and those of the exuviae of Nos. 25, 40 and 41. It therefore died in the last larval instar and its (preserved) exuviae are the penult, tertiult, quartult and quintult respectively (Calvert, 1925, 1928, pp. 14-15, footnote 4). Larva No. 23, collected August 22, 1909, passed through five moults the later four of which correspond to the four of No. 32, while the other or earliest exuvia is, therefore, the sextult. We have also larva No. 28 and its exuvia which appear to be of the penult and tertiult instars respectively. Some additional larvæ found in nature correspond to the reared ults. We obtain therefore, Table IX, similar to Table III. We possess fifteen larvæ of apparently the same species as these exuviae, which, by interpolation in Table IX,

¹⁶ Compare his remark quoted *antea*, page 10, footnote 9.

TABLE IX
RANGE OF CHARACTERS OF LARVAL EXUVIÆ OF *ANAX* AMAZILI REARED THROUGH FIVE MOULTS OR FEWER

Exuviae	Inferior Appendages, Mm.	Cercoids, Mm.	Front Margin, Hind Wing Rudiment, Mm.	Antennal Segments	Tarsal Segments	Male Gonapophyses, Mm.	Female Gonapophyses, Mm.	Width of Head, Mm.	Total Length, Mm.
Sextult (8th) No. 23 ♀	1.88	.41	.57	6	3		8th .06 9th .14	4.17	18.5
Quintult (9th) No. 32 ♂	2.37	.65	.78	6	(lost)	.09	8th .26 9th .30	4.42	21±
No. 23 ♀	2.45	.65	.90	6	3			4.58	24
Quartult (10th) No. 32 ♂	3.11	.82	1.23	(lost)	3	.14	8th .51 9th .51	4.91	28±
No. 23 ♀	3.27	1.06	1.47	6	3			5.64	27
Tertult (11th) No. 32 ♂	4.00	1.39	1.96	7	3	.17	8th 1.06 9th .74	5.89	34
No. 23 ♀	3.93	1.55	2.29	(broken)	3		8th 1.47 9th 1.23	6.54	33
No. 28 ♀	4.50	1.64	2.70	7	3			6.95	42
Penult (12th) No. 32 ♂	5.24	2.13	4.09	7	3	.31	8th 1.88 9th 1.55	7.94	42
No. 23 ♀	5.15	2.13	4.58	(lost)	3			8.18	(in fragments)
Ult (13th) Nos. 25, 40, 41 ♂	6.30-5.97	3.76-3.68	11.0-10.5	7	3	.49-.41	8th 2.45-2.36 9th 2.55-2.45	9.42-9.05	52-46
3 ♀ ¹⁷	6.22-5.47	3.59-3.02	11.0-10.0	7	3			9.24-9.05	50-49

¹⁷ Not reared, collected in nature.

In parentheses after the name of each exuvia, sextult, quintult, etc., is placed the corresponding number of Table III for *Anax junius*.

or by analogy with Table III, probably belong to the following instars: Octavult (6th) 5, 2♂, 1♀, 2?; sextult (8th) 1♂; quintult (9th) 1♀; tertiult (11th) 1♂, 2♀; penult (12th) 1♂, 1♀; ult (13th) 2♂, 1♀; of the last three one died in the act of transformation, one just before transformation as evidenced by the imaginal parts clearly visible immediately beneath the cuticle.

What has been said under the second section of this paper on the structural changes in the exterior of the larva of *A. junius* from the sixth to the thirteenth instars applies to the corresponding instars of *A. amazili* with the following exceptions: The narrowing of the hind margin of the vertex in some final exuviae results in its being only .36 of the maximum width of the same sclerite between the eyes.

No attempt has been made to determine the number or size of facets of the compound eyes.

Changes in the distal margin of the mentum of *amazili* between two larval instars, octavult and ult (presumably = sixth and thirteenth), are shown in pl. I, figs. 21 and 22, 23; the articular lobe becomes more convex than in *junius*. The depth in millimeters of the secondary ligular cleft in the exuviae of *amazili* listed in Table IX is as follows: Sextult (8th) ♀ .03; quintult (9th) ♂ .047, ♀ .064; quartult (10th) ♂ .062, ♀ .078; tertiult (11th) ♂ .078, ♀ .078-.094; penult (12th) ♂ .125, ♀ .14; ultimate (13th) ♂ .17?-.20, ♀ .11-.26. They show, as do our figs. 8-13 for *junius*, that this depth increases with the successive instars.

The right labial palp and distal mental margin of the quintult exuvia of larva No. 23 are figured by Calvert, 1928, pl. II, fig. 16.

The truncated shape of the end or fixed hook of the labial palp, present only in the first five instars of *junius* is characteristic for all the instars of *amazili* of which material is at hand (Pl. II, figs. 30, 31); the "produced and pointed" inner distal angle is more acute in *amazili* than in *junius*. In larva No. 39, last instar, of *amazili*, fourteen crenulations are visible on the distal end of this segment.

The length of the mid-dorsal abdominal process (.48 mm.) exceeds its width at base (.42 mm.) in the sixth instar and is more than half as long as the cerci in the eighth instar.

Traces of the copulatory apparatus and of the inferior abdominal appendage of the male imago are barely visible in the tertiult (eleventh) instar.

The color changes in the larvæ of *A. amazili*, as made out from the alcoholic material, are as follows:

Sixth Instar (Pl. IV, figs. 47, 48).—Body generally brown with the following pale: Clypeus, a central spot on the frons partly divided into an anterior and a posterior lobe, an anterior postantennal spot extending laterad to eye margin, a posterior postantennal spot connected with a mid-dorsal spot on the vertex, a lateral border behind each eye (the trachea which parallels the hind margin of the head each side is fuscous and shows through the head wall), a mid-dorsal thoracic stripe (bordered apparently on each side by fuscous of the two main dorsal tracheal trunks showing through the body wall), a lateral area on meso- and meta-thorax in which the wing rudiments lie, abdominal segment 1, or 1 and 2, an interrupted mid-dorsal stripe on 2-7 or 8, expanded among the dorsal puncta of 6 and 7, and bands on the legs. In all five larvæ, segments 8-10 are the darkest of the abdomen and 1 or 2, 5 or 6-7 the palest, which is in contrast to the condition described for *junius*. Tergal muscle markings are present on some or all of segments 3-8.

Eighth Instar.—Larva *c* (S. Isidro de Cartago, September 20, 1909). Similar to that described for the sixth instar except: Pale anterior postantennal spot is more sharply delimited behind and does not so evidently extend laterad to the eye, a mid-dorsal longitudinal brown double line dividing the pale mid-dorsal vertex spot, a small pale spot immediately behind the posterior mesal angle of each eye; some brown on meso- and meta-pleura above leg bases; pale mid-dorsal stripe absent from eighth abdominal segment; dorso-lateral and lateral puncta visible on 2-8, dorsal puncta on 3-8, lateral scars on 2-9; differences in ground color of

abdominal segments not strongly marked, but 8-10 are a little darker than 7 on both dorsal and ventral surfaces, but hardly if any darker than 3-6.

The sextult exuvia of No. 23, however, has abdominal segments 1-2, 8-10 uncolored, 3-7 much darker (brown) than the others, their anterior and posterior margins pale, abdominal appendages almost as dark as 3-7; there are slight brown markings on the thoracic segments, a little darker on the dorsum of head.

Ninth Instar (Pl. IV, figs. 49, 50).—Larva g (♀ Cartago, October 25 or 27, 1909). Like description of larva c, eighth instar, except: An elongate brown spot in the middle of the pale mid-dorsal vertex spot, a small pale spot behind the posterior margin of eye, a pale line on each side at right angles to hind margin of head about as far from the pale mid-dorsal vertex spot as the latter is wide, mid-dorsal pale stripe on thorax reduced to a line bordered each side with light brown and much reduced on abdominal segments 3-5, absent from 8, a brown spot immediately in front of base of each wing-rudiment, two lateral longitudinal brown stripes on each side of thorax between wing-rudiments and coxæ and continued on to abdomen where they are not sharply defined. Abdominal segments 8-10 distinctly darkest, 3-5 next darkest then 2, 6 and 7, 1 least brown, but 1-10 all are brown, two (on 2) or four (on 3-9) dorsal puncta, dorso-lateral and lateral puncta and lateral scars on 2-8, patches of darker brown among the dorsal puncta of 3-5 and of 8; lateral scars present, but not as distinct, on 9; apical third of mid-dorsal appendage, adjacent parts of inferior appendages and most of the cercoids pale.

The quintult exuvia of No. 23 has abdominal segments 3-7 not darker than the others, the anterior margins of 2-8 paler, the posterior margins of 3-8 with ten longitudinal whitish lines, 1 with four dorsal and the dorso-lateral puncta; the dorsal surface of head and thorax concolorous with the abdomen, pale markings indistinct.

The quintult exuvia of No. 32 has almost no coloring on

thorax or on abdominal segments 1 and 2, 8-10, 3-7 darker, their anterior and posterior margins as in No. 23.

Tenth Instar.—The quartult exuviae of Nos. 23 and 32 have abdominal segments 3-7 not darker than the others.

Eleventh Instar.—Larva *h* (♀ Cartago, October 25 or 27, 1909). Like description of 6th instar except: Tracheal colorings not visible in head and thorax, a brown spot on each side of the clypeus, central pale spot of the frons bordered posteriorly with a dark brown line, pale posterior post-antennal spot isolated from mid-dorsal vertex spot, markings of vertex and behind eyes as in 9th instar, the two lateral brown stripes of thorax described for 9th instar confluent here and there. Much of abdominal segments 1 and 2 covered by wing rudiments, pale mid-dorsal line visible on 3-7, not sharply defined. Abdomen largely brown, dorsal puncta (4) on 3-8 and (2) on 10 surrounded by an almost equally dark area on 3-5 and on 8, dorso-lateral and lateral puncta on 2-8, lateral scars on 2-9; small interrupted yellow stripes between dark brown mid-dorsal areas and the dorso-lateral puncta, between these and the lateral puncta, between these and the lateral scars and between these last and the brown of the lateral margin, on segments 2-6, less distinct or absent more posteriorly; as a whole segments 8 and 9 are darker than 6 and 7.

Larva *i* (♂ Cartago, August 28, 1909). Like above description except: Clypeus light brown, pale mid-dorsal spot of frons reduced to a line between (but perhaps not connected with) the pale anterior postantennal spots. Colors not as well preserved as in *h*, much paler throughout, no dark brown areas surrounding the dorsal puncta, no abdominal segments darker than the others.

Larva *j* (♀ Cartago, August 31, 1909). Much faded and much stretched, consequently showing more of abdominal segment 1 which has the dorso-lateral puncta.

The tertiult exuviae of Nos. 23 and 32 do not show abdominal segments 3-7 to be darker than the others.

The colors of the larvæ and exuviae of the two remaining

instars are not well preserved and seem to offer no additional information.

Descriptions of full grown larvæ of *amazili* have been published by Cabot (1881, p. 17), Byers (1927, p. 67) and Klots (1932, p. 17).

The collection belonging to the late Mr. E. B. Williamson, in the University of Michigan Museum of Zoölogy at Ann Arbor, contains final exuviae of a species of *Anax* collected by Mr. Jesse H. Williamson at Manaos, Brazil, in 1922. They are as follows: 1 ♀ "June 15, from 30' diameter pond in sand on hill side"; 1 ♂ 3 ♀ "June 20, Ponds in sand in 2d section Flores car line"; 2 ♀ "June 20, Swamp across car track from the Bosque"; 1 ♂ 5 ♀ "June 22, Ponds 1/2 way to Flores." The two male and five of the female exuviae were measured and minutely compared with the Costa Rican exuviae. The only differences revealed are that both sexes have slightly longer inferior appendages (♂ 6.46-6.54, ♀ 6.14-7.12 mm.), the females have slightly longer cercoids (3.27-3.60 mm.), the ratio of length of cercoids to that of inferior appendages is slightly lower (♂ .53-.56, ♀ .50-.53 *vs.* ♂ .57-.62, ♀ .51-.56 in the Costa Rican examples), and the width of the apex of the male projection is slightly less (.57 mm. *vs.* .7-.74 mm.). (Pl. II, figs. 37, 38.)

The only imago *Anax* hitherto reported from the vicinity of Manaos is the male type of *Anax concolor* Brauer. Mr. J. H. Williamson took such a male at Manaos, on June 16, 1922, which agrees throughout with Brauer's detailed description of 1868,¹⁸ except that the membranule is brown with no white. Hagen,¹⁹ although without having seen Brauer's type, considered *concolor* as a race of *longipes* Hagen. A comparison of Mr. Williamson's Manaos male with two males of *longipes*, one from Florida, the other from Staten Island, New York (taken by Mr. W. T. Davis), makes it clear that the three specimens are very similar. The two males from the United States show some differences from each other in the pattern of the abdomen and in the shape of the apex of

¹⁸ Reise der österreichischen Fregatte Novara, II, Neuropteren, p. 66.

¹⁹ Psyche, V, p. 304. 1890.

the superior appendages; both of them have only a longitudinal blackish *line* on the mid-dorsum of abdominal segments 3-7, due chiefly to the black denticles located there, while the Manaos male has a longitudinal mid-dorsal brown *band*, .5-1.5 mm. in width, on the same segments. Since the exuviae from Manaos are so similar to those of *amazili* from Costa Rica, while the imago from the same place is very close to *longipes*, it is evident that at least two species of *Anax* occur at Manaos. In view of this conclusion, the following note, in Mr. J. H. Williamson's handwriting, on the original envelope containing the Manaos male, is interesting: "Cruising over big pond in sandy soil in open. Only one seen to-day. Believe this was what J.W.S[trohm] missed in wood's trail yesterday. He differs."²⁰

VI. THE SUPPOSED LAST LARVAL EXUVIÆ OF *ANAX LONGIPES*

Prof. J. G. Needham (1904, page 695 and pl. xl, fig. 1) described and figured "a single huge cast skin from Jamaica," in the United States National Museum, which he "referred by supposition to this species," adding: "There is in this case, however, no satisfactory assurance that the reference is correct." As his description indicates, this skin is much like that of *junius*. I believe that it is not *longipes* for the following reasons.

I have before me two male exuviae from Primos, Delaware County, Pennsylvania, collected by myself, August 7, 1925, and eight male, seven female exuviae collected by Mr. J. H. Williamson, at Enterprise, Florida, on April 18 and 22, 1921. Five of these males (including the two from Pennsylvania) and five females were examined in detail and differ from the 1904 description as follows:

Length ♂ 56.5-62 mm., ♀ 57-60; abdomen ♂ 40-43, ♀ 39-42; hind femur ♂ 12-13, ♀ 10-13; width of head ♂ 9.5-10, ♀ 10; width of abdomen ♂ 10-11, ♀ 10-10.5.

²⁰ Cf. J. H. Williamson, Papers, Michigan Acad. Sci. Arts and Lett., III, p. 417. 1923.

Labium differing from that of *junius* in that the lateral lobe (labial palp) is truncated at the end hook, almost rectangular at the antero-distal angle (not rounded off); median lobe (mentum) a little more prominent, divided in the middle of its distal margin to the chord of the arc by a distinctly open cleft, .34-.47 mm. deep. (Pl. I, figs. 24, 25; Pl. II, fig. 34.)

Additional details of these exuviae are given in the Synopsis, *postea*, page 46.

I have no direct evidence that these exuviae really are *longipes*, but as this is the only remaining species of the genus known to occur in eastern North America, *junius* and *amazili* larvæ being accounted for, and as imagos of *longipes* have been taken at Clementon and seen at Lucaston, New Jersey,²¹ distant in a straight line from Primos not more than 19 miles (31 km.), and as Mr. J. H. Williamson took imagos of *longipes* at Enterprise, Florida on April 17 and 20, 1921 (E. B. Williamson *in litt.* Nov. 2, 1932), it seems likely that this association is correct. It is indeed remarkable that, if these exuviae be *longipes*, they should be so much larger than those of *junius* and *amazili* than the imagos of *longipes* are larger than the imagos of the other two species. If these exuviae had been found in California, it would be natural to refer them to *A. walsinghami*, the largest of all North American *Anax*. Byers (1927, p. 66) has described a female larva from California, which he refers to *walsinghami*. His description agrees with our two Primos exuviae in many details, but his figure of the mental margin is different (see our pl. I, figs. 24, 25). As imagos of *walsinghami* are, I believe, unknown east of California, it would be a greater stretch of the imagination to suppose that strays occurred in Pennsylvania and in Florida than to refer these exuviae to *longipes*. The cast skin from Jamaica which Prof. Needham referred to *longipes* is, I suggest, a large *junius*, as imagos of the latter have been found in Cuba and in Martinique. I communicated these views to Prof. Needham before the publication of his recent *Handbook* and he has adopted them therein (1929, p. 128).

²¹ Ent. News, xiv, 35 and xxvi, 334.

Mr. E. B. Williamson's collection contains also six male and seven female larvæ of *Anax* from Georgetown, British Guiana, probably from canals adjacent to the town. They were not collected by Mr. Williamson. They have the labial palp shaped as in *amazili* and *longipes* and, by comparison with the former, appear to be of the ninth and tenth instars. Some of their dimensions are: secondary ligular cleft .03-.09 mm. deep, cerci 2.45-2.94 mm. long, cercoids .53-.82 mm. long, front margin of hind wing rudiment .67-1.31 mm., gonapophyses of the ninth segment .16 mm. ♂, .30-.55 mm. ♀, width of head 4.00-4.66 mm., total length 18.0-27.5 mm. As no larval instars of *longipes* other than the last are known, it seems impossible to decide whether these Georgetown larvæ are *amazili* or *longipes*.

VII. THE SUPPOSED LARVA OF *ANAX GUTTATUS*

An alcoholic female larva of a species of *Anax* is in the collection of the University of Pennsylvania labeled merely "Borneo Furness coll." It was doubtless collected by Dr. William Henry Furness, 3d, the anthropologist and student of orang-utan intelligence, on one of his visits to that island. The only species of *Anax* included in Dr. F. F. Laidlaw's *A Revised List of the Dragonflies (Odonata) of Borneo* (1931) is *A. guttatus* Burmeister. Cabot (1881, p. 16) has described nymphs from Ebon, Marshall Island, Pacific Ocean which he identified as probably *guttatus*. Needham has described and figured (1904, p. 695, pl. xl, fig. 2) some nymphs from Buitenzorg, Java, which he referred to *guttatus*. Mr. Lieftinck (1930, p. 328, fig. 8) has briefly described and figured part of the labium of a West Javan example. The present specimen agrees with these descriptions with the following exceptions. In comparison with that given by Cabot, the mentum is only 3.8 times as wide as long, assuming that it was this portion of the labium he had in mind when he wrote "more than 4 times longer than the breadth of base," and the ovipositor seven-tenths as long as segment 9 instead of one-half. The proximal and distal segments of the labial palp,

measured on their lateral margin, are 1.55 and 2.86 mm. long in the Bornean larva, as contrasted with Mr. Lieftinck's measurements of 1.80 and 2.65 mm. respectively. The ratios in the two specimens are, consequently, 1.845 and 1.472, which do not approximate sufficiently to enable a specific character to be drawn from them.

The following additional data on the Bornean larva are appended: The imaginal labium has begun to withdraw from the larval labium.

Total length 50 mm., width of head 9.00, hind margin of vertex 1.55, seven antennal segments, maximum width of mentum 5.73 mm., of its median lobe 2.13, of an articular lobe 1.64, the secondary ligular cleft only .04 mm. deep, a tooth about .012 mm. long each side, distant .05 mm. from the middle line (Pl. I, figs. 15, 16), front margin of the hind wing rudiment 11.5 mm. long, three tarsal segments, mid-dorsal abdominal process 5.81 mm., laterals (cercoids) 2.70, inferiors (cerci) 6.38, gonapophyses of the eighth segment 2.04, of the ninth 2.13. Color generally reddish brown (possibly due to some earlier preservative), markings not distinct other than the slightly darker tergal abdominal muscle markings and the ill-defined pale greenish posterior margins and posterior lateral angles of segments 1-8 on both dorsal and ventral surfaces.

VIII. TAXONOMIC CHARACTERS OF THE LARVÆ OF ANAX

The family, subfamily and generic characters of the larvæ of the *Æshnidæ*, *Æshninæ* and genus *Anax* have been given by recent authors²² as follows, modified by our present results:

Family *Æshnidæ*: *Body elongate, head wide. Labium flat, or nearly so, without raptorial setæ (except in Cordulegaster and Gynacantha). Hind legs not reaching the end of the abdomen. Abdomen forming more than half the length of the body, widening from the base to the seventh segment, thence narrowing to the end.*

²² Garman 1927, Needham 1930, Needham and Heywood 1929, Rousseau, Lestage and Schouteden 1921, Tillyard 1916 and 1917.

Subfamily *Æshninae*: Body four to six times longer than wide, robust, smooth. *Head flattened, subquadrangular. Eyes wide, occupying the antero-lateral angles of the head, very prominent, prolonged caudad and mesad in a triangular lobe. Antennæ short, slender, setaceous, 7-segmented (6 in Epiaschna). Labium flattened, covering the mouth parts as far as the labrum, the median lobe (mentum) with the anterior margin convex and with short hairs, lateral lobes (labial palps), short, straight, movable hook strong and large. Prothorax small. Legs slender, femora and tibiæ of the same leg subequal, tarsi more than half as long as the tibiæ, three-segmented, proximal segment very short, claws two, short, incurved, acute. Above the attachments of the first legs are two prolongations (supra-coxal processes) which form a more or less open angle between themselves. Wing-rudiments not strongly divergent. Abdomen elongate, without tubercles or spines on the mid-dorsal line (except in Nasiaschna), infero-external angle of some of the hind segments prolonged in a spine.*

Genus *Anax*: *Hind angles of the head broadly rounded, lateral spines on abdominal segments 7-9 only, inferior terminal abdominal appendages (cerci) longer than the ninth and tenth segments together, the mid-dorsal notched at apex, the laterals (cercoids) never more than seven-tenths as long as the cerci, usually about half as long.*

Of the above characters, those italicized are possessed by the larva of *Anax junius* from its first instar onward; the others are acquired at a later period than the first instar. All of them apply to the fully grown larva. Changes in some of these characters, from the first to the last larval instar, have been discussed in the second section of this paper.

The generic character of *Anax* that the *lateral abdominal spines* are confined to segments 7, 8 and 9 holds true for most larvæ and exuviæ known to have come from eggs of *junius*, which I have examined. Some exceptions, in which a much smaller spine is present on segment 6 also, have been found. Measurements are given in

TABLE X

LENGTH IN MILLIMETERS OF THE LATERAL ABDOMINAL SPINES OF LARVÆ OF *ANAX*
JUNIUS REARED FROM EGGS

Instar	Individuals Measured	Segment 6	Segment 7	Segment 8	Segment 9	Total Body Length
First	1 larva 4 exuviae	.005 † .003 ‡	.012-.023	.018-.032	.023-.032	2.37-2.70
Second	2 larvæ 3 exuviae	.0078 § .0065 †	.013-.032	.03 -.039	.0195-.039	1.96-3.11
Third	2 larvæ 1 exuvia	.0065 §	.03 -.038	.046-.065	.046 -.059	2.70-3.35
Fourth	1 exuvia	.006 ‡	.03	.07	.068	3.68
Fifth	1 "	.007 ‡	.078	.14	.14	7.36
Sixth	1 "	.02 ‡	.156	.23	.23	10.14
Seventh	1 "	.03 ‡	.218	.31	.34	14.00

† in No. 2.

‡ in No. 3.

§ in No. 4.

Where a "spine" is present on segment 6, it is the hindmost of a series of teeth on the lateral carina. Such teeth are present on the lateral margin of the spines themselves of 7-9 in the fifth and following exuviae.

While no special search has been made for last exuviae of *juni*us with lateral spines on abdominal segment 6, two such have been found. One female, Primos, Penna., July 1, 1913, has a spine .47 mm. long on the right side of 6, but no trace of any on the left side; the right spine of 7 is .94 mm. long. One female from Smithson's pond, Cheyney, Penna., October 18, 1928, has a spine on each side of 6, .11 mm. long right, .12 mm. left; the spines on 7 are .94 mm. right and .87 mm. left.

The interest of the existence of a lateral spine on 6 of *Anax* is that one of the chief differentials of genera of this subfamily is that *Anax* does *not*, while *Aeshna*, etc., *do*, possess a lateral spine on 6. Since this is almost the only differential available in the early instars, it becomes a practical question as to whether it can be relied upon as a sure means of identification. Among the material received from Prof. Kennedy, individuals have been found with a spine of the following lengths on 6:

Second Instar < .006 (No. 141),

Third Instar .006 (No. 131), .007 (No. 34), .010 (No. 132),
.018 (No. 141)

Fourth Instar .0065 (No. 131), .009 (No. 152), .013 (Nos.
132, 134, 158)

Fifth Instar .0097 (No. 160), .0227 (No. 158)

With the above data may be compared the following measurements made from larvæ of *Æshna luteipennis*, reared from eggs at Cartago, Costa Rica, in October, 1909:

TABLE XI

LENGTH IN MILLIMETERS OF THE LATERAL ABDOMINAL SPINES OF LARVÆ OF *ÆSHNA*
(*CORYPHÆSCHNA*) *LUTEIPENNIS* REARED FROM EGGS

Instar	Individuals Measured	Segment 6	Segment 7	Segment 8	Segment 9	Total Body Length
First.....	5 larvæ	.026-.036	.046-.052	.065-.075	.052-.08	2.05-2.21
Second....	5 "	.0195-.026	.052-.065	.052-.091	.065-.085	2.54-3.76
Third.....	2 exuviae	.032-.046	.091-.117	.14-.15	.124	(distorted)
Fourth....	1 "	.039	.104	.20	.156	7.77
Fifth.....	1 "	.06	.15	.23 (left) .27 (right)	.176	9.73

No other material of early instars of the genus *Æshna* is accessible to me. It may be that in other species of that genus the lateral spines of segment 6 are shorter than they are in *luteipennis*. In view of the facts that a minute spine is present on the sixth segment of the first, fourth, fifth, sixth and seventh instars of larva No. 3 of *Anax junius* (the larva raised from egg to imago), that this spine is so much smaller than the spine on segment 7 in each instar than is the case in *Æshna luteipennis*, and that the spine is considerably and absolutely smaller than in that species, I have referred the specimens mentioned above as having a spine on 6, received from Prof. Kennedy, to *Anax junius*.

IX. SYNOPSIS OF THE LARVÆ AND EXUVIÆ OF THE LAST PREIMAGINAL INSTAR OF SOME SPECIES OF *ANAX*

The ontogenetic change in the shape of the end hook of the labial palp of *Anax junius* from truncated to rounded,

shown in our fig. 27, pl. II, suggests that those species of this genus which possess the truncated form in the last larval instar are phylogenetically older. The depth of the secondary ligular cleft also differs among the species, but here the ontogeny in *junius* and in *amazili* compels us to consider the deeper cleft to represent a younger condition. On these two bases then the following species are arranged.

External distal angle of end hook of labial palp almost a right angle, hardly rounded off (Pl. II, figs. 31, 32, 34).

Secondary ligular cleft .12-.28 mm. deep, not reaching to the chord of the arc formed by the median mental lobe (Pl. I, figs. 19, 20, 22, 33); cerci 5.66-6.54 mm. ♂, 5.47-7.12 mm. ♀, cercoids .53-.7 ♂, .50-.55 ♀, as long as the cerci, ♂ projection .28-.32 as long as the cercoids (Pl. II, figs. 37, 38); total body length 46-52 mm. ♂, 47.0-53.5 ♀ (including Costa Rican and Manaus examples) *amazili* Burmeister (Louisiana to Rio Janeiro and the Galapagos).

Secondary ligular cleft .34-.47 mm. deep, reaching to the chord of the arc (Pl. I, figs. 24, 25); cerci 7.8-8.5 mm. ♂, 7.9-8.4 mm. ♀, cercoids .47-.53 ♂, .42-.48 ♀ as long as the cerci, ♂ projection of the mid-dorsal process .28-.33 as long as the cercoids (Pl. II, fig. 39); total body length 56.5-62 mm. ♂, 57-60 mm. ♀ *longipes* Hagen (Massachusetts to Matto Grosso, Brazil).

Secondary ligular cleft .75 mm. deep, reaching proximad beyond the chord of the arc; inferior appendages (cerci) 7 mm. long, laterals (cercoids) .57 as long as the cerci; total body length 58 mm. ♀, ♂ unknown.²²

walringhami McLachlan (California, Mexico, Guatemala).

External distal angle of end hook slightly rounded off (Pl. II, fig. 33), secondary ligular cleft not reaching to the chord of the arc, etc. (Pl. I, figs. 17, 18).

Cerci 6.14-6.71 mm., cercoids .51-.56 ♂, .47-.52 ♀, as long as the cerci, ♂ projection almost half as long as the cercoids, apex straight (Pl. II, fig. 36); ♀ gonapophyses reaching to at least two-thirds of the length of the ninth segment; secondary ligular cleft .16-.08 mm. deep; total body length 45.5-59.0 mm.²⁴

imperator Leach (Europe, western Asia, Africa).

Cerci 5.5 mm., ♂ projection little more than one-third as long as the cercoids, apex broad, emarginate in a shallow curve, ♀ gonapophyses hardly reaching to half the mid-ventral length of the ninth segment; total body length 47-50 mm.²⁴

parthenope Selys (Central and Southern Europe, Asia).

Cerci 5.5 mm. long, cercoids .44 as long as the cerci, ♂ projection one-third as long as the cercoids; total body length 46 mm. ♂, ♀ unknown.²⁴

(*Hemianax*) *papuensis* (Burmeister) (Australia, New Guinea).

External distal angle of end hook strongly rounded off (Pl. II, figs. 27, 29), secondary ligular cleft not reaching to the chord of the arc, etc.

Secondary ligular cleft .04 mm. deep, distal mental margin a little more arched (Pl. I, figs. 15, 16); cerci 6.38 mm., cercoids .42 as long as the cerci; total body length 50-60 mm. (these data from ♀ only, ♂ data in the literature incomplete). *guttatus* Burmeister (East Indies).

²² Diagnosis according to Byers, 1927, p. 66.

²³ Diagnosis based on 4 ♂, 2 ♀ exuviae from Indre, France, collected by René Martin, and on Ris 1909, p. 58.

²⁴ Diagnosis according to Ris, 1909, p. 59.

²⁵ Diagnosis according to Tillyard, 1916, p. 68.

Secondary ligular cleft .07-.14 mm. deep, distal mental margin a little less arched (Pl. I, figs. 13, 14); cerci 5.24-6.30 mm. ♂, 5.32-5.90 mm. ♀, cercoids .44-.48 as long as the cerci, ♂ projection .45 as long as the cercoids (Pl. II, fig. 35); total body length 41.5-49.0 mm. ♂, 44-50 mm. ♀ *junius* Drury (North and Central America, West Indies, Hawaiian Islands, Kamtschatka, China).
Secondary ligular cleft ca. .23 mm. deep, other data lacking.

fumorus Hagen (East Indies).²⁷

In the last exuviae the cercoids of the males have the antepical sinus of the inner margin deeper than in those of the females, the apex being incurved a little more in the former sex. This holds true for Costa Rican examples of *amazili*, for *imperator* and for *junius*, but not for *longipes* nor the specimens from Manaos which have been placed with *amazili*.

X. THE SEASONAL DISTRIBUTION OF SOME SPECIES OF *ANAX*

In the North Temperate Zone

Anax junius (Drury).—In Southeastern Pennsylvania the earliest and latest dates on which this species has been seen flying are March 28 (1907,²⁸ Mr. Charles Liebeck) and October 16 (1889, P. P. Calvert). It has been observed pairing or ovipositing on May 1, June 15, 19, 22, 28, July 6, 13, August 25, 31, of different years. Eggs laid June 28, 1889, began hatching on July 6; those laid July 13, 1926, on or before August 1 (Calvert 1929). The minimum embryonic period, therefore, may be but eight days. With oviposition as scattered throughout the warmer season as the above cited dates indicate, it is manifest that at any one time within the year one will find larvæ of very different instars. The data for this area derived from various years are as follows:

Instar

- 1 May, July 6+, Aug. 1-8, Oct. 7
- 2 Aug. 10-22
- 3 Aug. 13-Sept. 6
- 4 Sept. 5-9

²⁷ Diagnosis according to Lieftinck, 1930, p. 328.

²⁸ Cf. Davis, W. T., that "he had seen it [*junius*] numerous on Staten Island on March 29 and 30, 1907, an early date for the species." *Bull. Brooklyn Ent. Soc.*, xxi, p. 207. 1926.

- 5 July 10, Sept. 5, **20**, 23
- 6 July 10, Aug. 11, 18, Sept. **24**, Oct. 7
- 7 July 10, Aug. 11, 18, Sept. 3, 12, 23, Oct. 3
- 8 July 10, Aug. 11, 18, Sept. 12, *20*, 23, 25, Oct. 7, **17**, *18*
- 9 Feb. **25**, April 2, July 10, Aug. 11, 18, Sept. 12, 25, Oct. 7
- 10 Mar. **20**, Apr. 2, May 7, July 10, Aug. 11, 18, Sept. 12, 23, 25, Oct. 11
- 11 Apr. 2, **17**, May 3, 7, Aug. 8, 11, 18, Sept. 25, Oct. 7, 11
- 12 Feb., Apr. 2, May 7, **8**, June 1, Aug. 11, 18, Sept. 25, Oct. 11
- 13 May, June 3, *14*, **19**, July 1, 10, Aug. 7, *12*, *18*, 25, Sept. 5, 7, 9, *10*, 12, *19*, 23, 25, 25, Oct. 7, 11, *18*

The dates in bold face are those of the ecdyses of larva No. 3 reared from egg to adult, those in italics of exuviae of other reared or collected ²⁹ material. A collection made in Smithson's pond, Cheyney, Penna., Aug. 18, 1930, contained larvæ of all instars from the 6th to the 13th inclusive; some of these are shown in our pl. III. A lot from Primos, Penna., on Sept. 23, 1913, had representatives of the fifth, seventh, eighth, tenth and thirteenth instars; one from Smithson's pond on April 2, 1933, includes instars 9-12.

Prof. Kennedy's 1917 collections in the vicinity of Ithaca, New York, show the presence of all instars, from the first

²⁹ Some of these collected exuviae were found floating in water and the question arises: How long had they been shed before they were collected? The following simple experiment gives the probable maximum time. Two *junius* and three Libelluline exuviae floating in Smithson's pond, Cheyney, Pennsylvania, May 14, 1933, were placed in a quart jar more than half-full of water of the pond. The jar was kept closed, in my study, at a north window where, in the late afternoons, the sunlight fell directly upon it. On May 24, one Libelluline exuvia was at the bottom of the jar but rose to the surface later in the day. On June 7 all the exuviae were more or less disintegrated and many of the sclerites were lying on the bottom of the jar; some fragments, with air bubbles within them, were floating. A *Limnaea*, 6 mm. shell length, was on the side of the jar and a few Cyclopoid crustacea were swimming in the water. There was no odor of decomposition. The hydrogen ion content of the water, determined on June 19, by Mr. Clifford A. Angerer, was 6.8 (bromthymol blue indicator) or 6.7 (phenol red). In this experimental jar, where the water was undisturbed, flotation of entire exuviae, therefore, occupied less than 23 days. In nature where disturbing conditions due to wind, rain, colliding bodies, etc., prevail, injury and sinking probably come sooner.

to the thirteenth inclusive, between July 12 and August 20. He obtained first instar larvæ July 27, Aug. 1, Sept. 3 and 16.

Appearance of the imago of *junius* in Indiana extends from March 24 to Oct. 10, and Montgomery saw this species pairing on March 31, 1925 (Williamson 1917, Montgomery 1927). A manuscript note of Prof. Kennedy's records a "female ovipositing at Branchippus Pond, Columbus, Ohio, on March 25." Whedon (1914) observed *junius* ovipositing in Minnesota (44° North Latitude) "as early as March 5 . . . in the ponds, usually the smaller and more shallow ones and the worn condition of these females suggests that they had hibernated through the winter." Kellicott (1899, p. 78) says: "This species has been taken at Columbus, Ohio, as early as March 21st and has been observed on the wing during the first days of November." In an earlier paper (1895), p. 212, is a fuller statement on the first date given as follows: "This year (1894) it was plentiful along an old river bed on the State University grounds, on March 21. Several pairs were seen on this date, flying about in union ovipositing. . . . On March 23 it turned cold, and remained so until April 15. On the 16th, *Anax* was again abroad, apparently uninjured by frost, ice and snow of the preceding three weeks." Were the latter individuals the same as those flying on March 21?

Williamson's (1903) earliest and latest dates for the imagos in the vicinity of Nashville, Tennessee, are March 17 and October 14. Farther south one would naturally expect them to be flying earlier and Blatchley (1932) reports them at Sarasota, Florida, on Feb. 17, 1911, while Skinner took a male at Guantánamo, Cuba, Feb. 13, 1914 (Calvert 1919b, p. 357). For the other end of the year are the dates December 5, Alachua or Dade County, Florida (Byers 1930, p. 12), Oct. 27, on the northern coast of Porto Rico, and Nov. 28 on the island of St. Thomas (Klots 1932). At Galveston, Texas, I saw many *junius* pairing, and females, with males attached to them, laying eggs on Sept. 26, 1906.

The Baja Californian and other Mexican records of *junius*

range from April to October (Calvert 1895; 1901-08, for dates see Table I in the Introduction). The recorded localities on the mainland of Mexico are all above 1100 meters, but those from the peninsula of California are both near sea-level and higher. Hagen (1890) gives Costa Rica as within the habitat of *junius* but without citing localities or specimens. Mr. Banks writes (May 18, 1933) from the Museum of Comparative Zoölogy: "There is no specimen of *Anax junius* from Costa Rica in the collection here; the only Central American specimens are three from Matamoros." During a year spent in Costa Rica I saw no *junius*, nor has any other collector sent me specimens from that country.

Prof. Needham (1924) has given an account of some significant observations on *junius* at three ponds at the head of Laguna Canyon, in the San Joaquin hills, south of Los Angeles, California, at an altitude of 325 feet. They are "natural bodies of permanent fresh water," but "not quite permanent for after a succession of dry seasons (as in the years 1919-20-21) the water in them disappears." At these ponds he says that *junius* is "very abundant, transforming and flying most of the year. Nymphs of all sizes present in the water at all times and in great numbers. . . . There is always a great excess of the very young nymphs for they are great cannibals; the larger eat the smaller." On August 18, he obtained 150 exuviae of *junius* in a distance of 10 meters.

The Asiatic records of *junius* which supply time data appear to be Petcheli (Pe-chi-li) Bay, April (Hagen 1890, p. 306) and Tsche-kiang, April (Schmidt 1931, p. 185), both in China.

The bodies of water at which *junius* oviposits are, as the above quotations and the writer's personal experience indicate, often small and shallow and hence liable to disappear in prolonged periods of dry weather. There are apparently no data as to the situation and fate of the larvæ under such circumstances or (in winter) when the water is frozen. Although these larvæ usually live among vegetation at or near the water's surface, we assume that in droughts and

in winter they burrow into the mud of the bottom or into deep water vegetation where this is possible (Cf. Wesenberg-Lund 1912, pp. 292-295, 1913, pp. 385-395); the facts, however, as well as the conjectured hibernation of the adults remain to be ascertained.³⁰

The data on seasonal distribution of *junius* given above, seem to justify the conclusions that, when minimum air temperature reaches and remains above 33° F. (0.6° C.),³¹ imagos will be in evidence and may be expected to oviposit; that there will be a more or less frequent succession of larvæ as long as water and its contained food are present; that in any one permanent body of water, otherwise suitable, there will be found, on any one day, larvæ of many different instars; that transformation to the imago stage will occur at frequent intervals within, but probably considerably above, the temperature limits stated and that, except within these limits, there is no correlation of the appearance of the imago with any one definite time of year.

Several writers have advanced the opinion that the development of *junius* from egg to adult may be accomplished within a few months. Thus Paul Fischer (1891) wrote: "In Franklin Park, in this city (Columbus, O.), a small lake was dug last winter in a place which was before entirely dry and well-drained, and during the last of April and the first of May this lake was filled with water from the city water-works

³⁰ This statement is intended to apply to conditions in the United States. For Australia, there is the observation by Tillyard (1916, p. 69): "In August, 1906, when a small pond near where I was living dried up, the damp water weed was simply alive with nearly full-fed nymphs of this species [*Anax papuensis* Burm.], which I picked up by the score. They were quite unable to withstand drought, and within a few days were all dead. This drought caused the species to become quite rare around Sydney for two years, but in 1908 it was fairly common again."

³¹ The daily minimum air temperature at Philadelphia in March, 1907, was below freezing until the 9th, when it rose to 35° F., but fell below freezing thereafter until the 13th, remaining above freezing for the remainder of the month, attaining 42°, 40°, 59°, 45° and 46° on the 14th, 22nd, 23rd, 27th and 28th respectively, dropping to 33° on the 19th, 21st and 26th. The 28th was the day on which the first *junius* was noted. In October, 1889, the daily minimum sank to 36° F. on the 7th, 34°, 29° and 29° on the 15th, 16th and 17th respectively, but stood at 46° on the 8th and 50° on the 14th. The 16th was the last date on which *junius* was observed. The temperature data were obligingly furnished by the Philadelphia Office of the Weather Bureau, U. S. Department of Agriculture.

pipes, which I am sure contain do [sic]²² dragon fly nymphs; and on the 30th day of August last, the shores of this artificial lake were literally lined with the exuvia of *Anax junius* nymphs; so they could not have been older than four months at the utmost. I saw the first *Anax junius* flying in the last week of April, and I think I am safe in saying that none appeared much earlier, as I was on a special look out for them." Kellicott (1895, p. 213) has cited this observation of Fischer's as appearing "to show that in this species, at least, imagos mature from eggs laid the same season."

Needham and Hart (1901, p. 48), referring to Kellicott, draw the conclusion that this indicates "the occurrence of two broods in a year. This is confirmed by one of our experiments, half-grown larvæ placed by Mr. Hart in a breeding cage, June 16, reaching the imago stage August 4. A noticeable reduction in the number of large nymphs and an increase of the younger ones about July 1 has been recorded in two different years. Young predominate in our October collections, and those taken early in spring are mostly of large size. The imagos attain greatest abundance in May. On May 19, 1894, the abundance of fresh exuviæ was considered worthy of record."

Mr. C. S. Brimley (1904) states: "During the late summer of 1902 the water in Green's rock quarry [North Carolina] dried completely up and remained so for at least two months. Unfortunately, I did not notice the dates when the pool dried and when it filled up again. On July 22 and August 10, 1903, I found in the quarry exuviæ of recently transformed *Anax junius*; . . . thus apparently showing that these four species had in this case completed their transformations in less than six months. The quarry had not had any water in it in the previous fall before late November at the earliest; thus the eggs of these species must have apparently been deposited in the spring of 1903."

To form an opinion on these suggestions, the data in Table XII may be examined. The 131 days occupied by the

²² Corrected to "no" on p. 214 of the same volume.

ninth instar of No. 3 is the winter diapause, spent in a moderately heated room and during which the larva fed. At other times of the year this instar may be reduced to 12 days, as indicated.

The four months during which Fischer supposed his *junius* to have developed from egg to imago total 122 days, which would have been sufficient for the laboratory larvæ to have developed from the eighth larval to the imaginal instar. His larvæ, out of doors, may have grown more rapidly. The first seven larval and the embryonic instars would require at least

TABLE XII
LENGTH IN DAYS OF THE INSTARS OF *ANAX JUNIUS*

Instar	No. 3 (Reared through 13 Instars)	Reared through 3 or Fewer Instars
Embryonic.....	18- July	8 July
1st larval.....	8+ July, Aug.	
2nd ".....	14 Aug.	3 Aug.
3rd ".....	15 Aug.-Sept.	
4th ".....	3 Sept.	2-6 July, Aug.
5th ".....	11 "	5 July
6th ".....	4 "	6-13 July, Aug.
7th ".....	9 "	17 Aug.
8th ".....	14 Oct.	17 Sept.
9th ".....	131 Oct. to Feb.	12-23 July, Aug.
10th ".....	23 Feb., Mar.	17-22 Aug.
11th ".....	28 April	17 Aug.
12th ".....	21 April to May	
13th ".....	42 May to June 19	

Total.....341 days

Total of the minima recorded for the several instars 177 days.
Additional data on No. 3 are given in Calvert 1929, pp. 238-240.

two months, according to Table XII. We are thus faced with the alternatives of supposing that the entire development was completed in four months as he thought, even with probably lower water temperatures in May, or that, in spite of his assurance to the contrary, larvæ of the eighth instar or younger, of a body length of 14 mm. or less, were introduced by the water-pipes or otherwise. Until positive evidence that the time required for development can be so much reduced, we incline to the second view.

Hart's half-grown larvæ occupied 49 days to reach the imago state on August 4. Half-grown larvæ are about 24 mm. long, and of the tenth instar. Table XII indicates minimum duration of 80 days for the last three larval instars and 110 for the first ten. Food, the higher temperatures of June and July and other laboratory conditions may have reduced the 80 days to 49, but it seems hardly likely that enough time could have been found previous to June 16, with the lower temperatures of April and March, to have made it possible that the imagos of August 4 proceeded from eggs laid the same year. If "the occurrence of two broods in a year" means two successive generations, the first the progenitor of the second, more precise breeding data must be produced to demonstrate that this takes place. This is a different view from that here advanced on page 55.

In Mr. Brimley's case, the account given does not exclude the possibility of eggs having been laid in late November, or even earlier, before the water in the quarry disappeared.

Prof. Kennedy, in a paper (*Ecology*, iii, p. 335. 1922) in which *junius* is the only species of the genus mentioned, says "*Anax* has speeded up its life cycle to three months," and makes an entry for *Anax junius*, "2-3 generations," in the table on p. 373, *Ecology*, ix, 1928. Prof. Walker wrote of *junius*: "It is the first dragonfly to appear in the spring, being on the wing in the vicinity of Toronto as early as the second week in April. It flies throughout May and June, but is seldom seen in July and August, appearing again however in September" (1908, p. 14). "Two stragglers were taken on the Station Island [Go Home Bay, Ontario], a female in good condition on June 26, '12 and a worn male on July 7. This is the latest date on which an adult of the spring brood was observed. . . . No individuals of the fall brood had yet made their appearance at the time the Station was closed in 1912 (Sept. 11)" (1915, p. 77). So also Prof. C. B. Wilson (1920, p. 188): "Some species of *Anax*, *Tramea*, and *Æschna* may have two broods during the year, in spring or early summer, and again in late summer or early fall, and conse-

quently would have two periods of maximum abundance"; but see his further remarks on pp. 191 and 251. None of these statements are accompanied by any supporting evidence.

To sum up: the existing breeding evidence does not admit of the occurrence of two successive generations within a year in the temperate North America. Under *continued* high temperature of both water and air, either in nature or in the laboratory, two generations per year may be possible, but this has yet to be demonstrated.

Anax imperator Leach and *A. parthenope* Selys, both palaearctic species, approach most nearly in their seasonal distribution to *A. junius*.

Portmann (1921) has reared *imperator* from egg to imago. His results as to the number (12) and characteristics of the larval instars have already been compared (pages 31-2, *anteâ*) with our own for *junius*. In the Rhine valley, in northern Switzerland, the adults appear at the end of May, oviposition takes place throughout June and July and in early August. Larvæ of the sixth, seventh and ninth to eleventh instars were found in the beginning of August. In November, the ninth to the twelfth instars were represented. He sums up the life history in these words: "*Anax imperator* ist also bei uns einjährig; seine Eier entwickeln sich in zwei bis vier Wochen, das Larvenleben währt etwa zehn Monate und die Flugzeit der Imago dauert wenige Wochen" (p. 31). By exposing larvæ of the eleventh instar in January and in October to 25° C. he obtained imagos in March and in January³³ respectively, with a larval period in the latter case of less than seven months, and concludes that it is not to be doubted that under favorable climatic conditions *Anax* can develop in half a year, that is, in that case be able to produce two generations (p. 35). Morton (1927, p. 228) was "inclined to think that in the [Alpes Maritimes, France] the

³³ W. Leonhardt (1913, p. 10) has the following note on this species: "Im Insektenhaus des Zoologischen Gartens zu Frankfurt a. Main aus Larven der dortigen Gegend gezogen; am 22 Januar 1912 was bereits das erste Tier geschlüpft [Joh. Englisch, i. lit.]."

species is double-brooded," but in a subsequent letter (18th December, 1927) to the author he wrote: "But looking to the results of your rearing *A. junius*, I am not sure that my conclusion is right and probably the correct view is that there is a continuous succession of emergences extending over the whole summer rather than two definite broods. Of course frost is practically unknown there at the Mediterranean level, and I expect the larvæ continue more or less active all the time."

In England, *imperator* has been seen in flight from May 11 to August 31 (Lucas 1902, p. 36, 1931, p. 176). Martin (1888, p. 100) recorded *formosus* (= *imperator*) at Poitou and Berry, France, from May 15 to Sept. 10. Gadeau de Kerville (1905, p. 171) quotes Lancelevée 1883, that this species occurs in the marshes in the neighborhood of Elbeuf, Seine-Inférieure, France, from May to September. The same dates are given for the province of Verona, Italy, by Garbini (1897, p. 60). Ten years of observation at Kiev in the Ukraine yielded May 25 and July 13 as the limits of appearance of *imperator* in that locality (Artobolevsky 1927, p. 88). Bartenev (1924, p. 16) observed this species in April and from June 3 to August 12 at lakes in the Caucasus Mountains and Bartenev and Popova (1928, p. 237) record a male as late as October 30 at Sukhum on the Black Sea in Transcaucasia, only 8° latitude farther south than Kiev.²⁴ Additional data on the seasonal distribution of *Anax* in Russia are given in various tables by Prof. Bartenev (1930).

Andres (1928, p. 27 and Table II) states that *imperator* is to be found in Egypt March to May and August to November, dates which suggest the possibility of two successive generations. In spite of the exceedingly small rainfall, although with a high temperature, throughout the year (Brooks, pp. 93-97, Kendrew, pp. 40-42, 82, 86), Andres contrasts the abundance of Odonata with the scarcity of other insects and connects it with the numerous ditches and canals (pp. 7, 8). McLachlan (1883, p. 181) examined

²⁴ The mean annual temperature of Kiev is 44.2°F. (6.8°C.), of Batum on the Black Sea south of Sukhum is 57.7°F. (14.3°C.). Kendrew, p. 192.

specimens from the Canary Islands taken in December. The African form, *imperator mauricianus* (Ramb.), which Ris (1921, p. 369) scarcely found worthy of sub-specific distinction, is reported by him from South African localities lying between 18° and 30° South Latitude, as occurring in the winged stage from September to March, and in August to November and in May in the Kilimandjaro district by Sjöstedt (1909, p. 31). Perhaps the specimens from Madagascar, collected in May and June, reported by Grünberg (1917, p. 485) as *imperator*, are of this form.

Anax parthenope.—Münchberg (1932) from his intensive observations in the Grenzmark, Germany, has likewise concluded that the larval life of this species is of one year (ein-jährig) in that region, and that the imago flies from the beginning of June until mid-September in central Europe. In Mesopotamia, as one would expect, *parthenope* is on the wing earlier, viz. March 20, 1918 (Morton 1919, p. 150), and later, October 15, 1918 (Morton 1920, p. 87). In Egypt Andres (1928, pp. 27 and Table II) mentions it only for May, September and October. Ris (1916, p. 63) records a female of *parthenope julius* Brauer taken in January in Formosa, Schmidt (1931, p. 185) and Sjöstedt (1932, p. 10), examples from China, in April, May, August and September, and Needham (1930, p. 76) a pair from Suifu in October, 1928. To *julius* Gerstaecker (1891, p. 7) referred a May female from Zanzibar and a June female from Bagamoyo, East Africa.

Tropical Species

Anax amazili Burmeister.—Hitherto unpublished data on the seasonal distribution of the imagos of this species in Costa Rica are as follows. Single individuals in each case are before me from Las Cañas on the Pacific slope, 15 meters altitude, June 8, 1923 (1 ♀, A. Smith), and from the following on the Atlantic slope: Cachí, 1000 m., August 9 (1 ♀) and November 2 (1 ♀) (C. H. Lankester), three which transformed at Cartago, 1451 meters, between August 31 and Sept. 10, December 7 and 10, and December 25 respectively,

from larvæ collected near Cartago, and one female captured at Cartago, October 7.³⁵

To these we may add the dates of last larval exuviae gathered in the Cartago neighborhood: September 20, October 7, 10, 11, 14, 25, 30, 31 (all in 1909, except Oct. 14 which is 1928) and one full grown larva which died in transformation November 9, 1909. Larvæ were collected at Cartago from August 22 to October 27; they represented instars from the sixth to the eleventh as computed *antea*, pages 32-34. The duration of the later instars are given in Table XIII, which may be compared with Table XII. There are no data for the length of the last larval instar.

TABLE XIII
LENGTH IN DAYS OF INSTARS OF *ANAX AMAZILI*

Instar	Larva No. 23 ♀	Larva No. 32 ♂	Month
Quintult (9th) larval.	8	5+	Aug. or Sept.
Quartult (10th) "	35	25±	Aug. or Sept. to Oct.
Tertult (11th) "	39	30	Oct. to Nov.
Penult (12th) "	72±	64±	Nov. to Jan.
	154±	124±	

The data in Table XIII compared with those for larva No. 3 in Table XII suggest that for the two larvæ of *amazili* reared at Cartago, Costa Rica, the winter diapause occurred in the penult (12th) instar, while that of *junius* No. 3 took place in the ninth instar. Had these two larvæ of *amazili* lived, it is likely that they would have yielded imagos in February or early March and we would thus have a seasonal

³⁵ As mentioned by previous writers (Calvert 1893, p. 250; Kellicott 1899, p. 78; Williamson 1900, p. 306), the female imago of *junius* differs from the male in the shape of the occiput, the male having the hind margin slightly concave, the female with the hind margin elevated and emarginated in the middle, or, as Kellicott expressed it, "twice tuberculate posteriorly." In *amazili* the occiput is very similar in the two sexes, its hind margin being concave. The occiput thus furnishes a diagnostic character between the females of these two species, added to which is another: *junius* female has supplementary lateral carinae on abdominal segments 5-10, *amazili* female on 4-10 (not always defined on 9); all the carinae on 5-6, both supplementary and normal, are more sinuous in *amazili* than in *junius*.

distribution of adult *amazili*, in the higher parts, at least, of Costa Rica very similar to that of *juni* in the more southern parts of the United States. The daily maximum and minimum temperatures at Cartago during our sojourn (Calvert, A.S. and P.P. 1917, pp. 501-511) were lowest in the months November to March. The larvæ of *amazili* obtained near Cartago were mostly from shallow pools. A description of the changes in these pools has been given (in the volume last quoted, pp. 75-76) to the effect that they increased in number and quantity of water from May to January, then decreased again. The shrinkage may explain, in part, why *amazili* either as imago or larva, was not seen in the vicinity of Cartago, from the beginning of the year 1910 on, but deeper pools, sufficient to maintain active larvæ, may have persisted slightly farther from the town. As A. Smith obtained an imago of *amazili* in June, in the lowlands of the Pacific slope of Costa Rica, Mr. D. E. Harrower took a male at Gatun, Canal Zone, Panama, also in June, and Garlepp a male in Panama in March (Ris 1918, p. 174), the species is to be looked for in low altitudes also. The fact remains that we did not see them. A remarkable testimony to the scarcity of this genus is contained in a letter of November 2, 1932, from the late E. B. Williamson, certainly a collector of great activity and experience in the American tropics: "For my part I have never seen an *Anax* in the tropics."

The remaining seasonal data recorded for *amazili* do not conflict with the views above stated. Thus Eisen and Vaslit obtained a female at Tepic, Mexico, 1036 meters, in October (Calvert, 1899, p. 387). Messrs. Schaus and Barnes got two females at light on June 2 and August 24 respectively, at Cayuga, Guatemala (ca. 45 meters, Calvert 1919a, pp. 32, 37). Gundlach (1888, p. 237), in spite of his long collecting experience in Cuba, mentions only a single specimen in that island—at Havana, October 1871. In the Island of Trinidad, West Indies, a female was found in June (Geijskes 1932, p. 102). Two full-grown larvæ were collected September 15, 1926, at Panzardi, Hato-rey, Porto Rico, by J. Garcia (Byers

1927, p. 67). In Ecuador, Prof. Campos (1922, p. 32) reports this species at Guayaquil from January to March. Mr. E. E. Austen took imagos on the Amazons in January at Santarem and in March at Mosqueiro (Kirby 1897, p. 614).

Anax longipes Hagen.—As indicated *antea*, p. 46, *longipes* has the greatest north and south distribution of all the American species of *Anax*. The existing data on seasonal distribution of the imago are chiefly from the United States:

Massachusetts: Woods Hole, Aug. 25, 1875 (Hagen 1890, p. 305).

New York: Long and Staten Islands, June 5 to Aug. 9, ovipositing June 25 (Davis 1914).

New Jersey: June 27 to Aug. 10 (Calvert 1910, p. 78, 1915, p. 334; Davis 1914, Montgomery 1933).

Pennsylvania: Poyntelle, June 30 (Calvert 1904, p. 317); Primos, last larval exuviae, Aug. 7 (*antea*, p. 39).

Ohio: near Cincinnati, June 2 (Dury 1900, p. 169); near Lake Erie, July 25 (Philpott 1913).

Georgia: Lee County, July 3, 1923 (Root 1924, p. 320).

Florida: Haulover, March 3 (Hagen 1890, p. 305); Enterprise, April 17 and 20 (*antea*, p. 40); Alachua County, April 26–May 30 (Byers 1930, p. 12).

Mississippi: Pass Christian, March (Davis 1914, p. 35).

Bahamas: Eleuthera, April 11–21 (Calvert 1909, p. 221).

Haiti: Feb. 14, 1884 (Hagen 1890, p. 305).

Mexico: Jalapa, Nov.; Amula in Guerrero, Aug.–Oct.; Pacific Ocean off Oaxaca, July 10, 1873 (Calvert 1901–08, p. 176; Hagen 1890, p. 305).

Here, as in *amazili*, the evidence is not very different from that presented for *junius*.

Anax immaculifrons Rambur.—Col. Fraser (1924, p. 464) writes of this species in Western India: "Larvæ are usually found in running water and at one time I was of opinion that they bred solely in rivers, but during 1922–23 I found larvæ in both the Ooty and Lovedale lakes, Nilgiris, and also in two ponds near Mercara, Coorg. In the first two weeks of March,

1922, I found several freshly emerged specimens hanging on reeds at dawn, around the banks of the Ooty lake. The first specimen observed on the wing appeared about the end of February. By the end of March great numbers were observed ovipositing in small streams on the kundahs, and from then onwards until the end of June the insect was tolerably common. The onset of the monsoon, in June, soon exterminates them but a second and more scanty brood appears at its end."

The end of the monsoon on the west coast is usually in October (Brooks, p. 104, Kendrew, p. 118). It will be interesting to determine, by actual breeding experiments, whether those *immaculifrons* which appear subsequently thereto are the descendants of individuals which oviposited in March and which themselves give rise to larvæ transforming in the following February, or whether this species seems, like *junius*, to exhibit a series of successive emergences instead of two consecutive generations within one year. Dr. Laidlaw (1924, p. 338) has recorded this species as occurring in August and September in Ceylon, Martin (1909, p. 213) in June in Lebanon, Syria.

Anax guttatus Rambur.—This species has been recorded as occurring in Ceylon in May, June, November, December and January (Kirby 1894, p. 558; Laidlaw 1924, p. 338), in Formosa in May and August, on the Chinese coast in June (Ris 1916, p. 63), in Hainan in August (Needham 1931, p. 231), in April, September and November in the Malay Peninsula (Laidlaw 1931, p. 207), and in August at Bettotan, Borneo (Laidlaw 1931*b*, p. 236).

Species of the Southern Hemisphere

Anax papuensis (Burmeister).—Dr. Tillyard (1916, p. 69) records having taken a female, in very fresh but mature condition, on the wing July 28, 1910, and says that pairing occurs from August to November. His account of the life-history, being comparative with that of *Æshna brevistyla*, would seem to imply that males at least are seldom seen after the end of

the year. Dr. Sjöstedt (1917, p. 18) quotes both sexes from North Queensland in January, February and May. Tillyard says that his observation of the effects of the drought of August, 1906, quoted *antea*, p. 51, footnote 30, "and the fact that half-grown larvæ can often be found in September, cause [him] to fix *two years* as the normal time for the larva to reach maturity . . . this species lives in absolutely still water. Its chief breeding places are water-holes, lagoons and the backwaters and billabongs of rivers. It occurs also on sluggish creeks and rivers, when the larvæ inhabit the deepest parts of large still pools, never being found around the edges, but only in the thick masses of reed or water-weed nearer the middle."

The mean temperature of Sydney for July is 52.7° F. (11.5° C.), for January 71.7° F. (22° C.); the average rainfall, 47.9 inches (1200 mm.), is distributed throughout the year (Brooks, p. 162). A species whose imagos appear in July might, therefore, be expected to be active throughout the year, unless drought persists.

Anax fumosus Hagen.—Recorded from the Island of Buru in February, May and June, all of 1921 (Lieftinck 1926, p. 277); in Sumatra in April and June (Ris 1927, p. 34).

Anax speratus Hagen.—The sparse South African dates from localities between 7° and 30° South Latitude, range from October to March (Ris 1931, p. 368).

South African data on other species are given *antea*, page 57.

The seasonal data brought together in the preceding pages may, it is hoped, serve as an incentive to observers throughout the world to test this question: Do the species of *Anax* generally show a seasonal distribution like that which has been suggested on pages 51 and 55 for *junius*?

XI. SUMMARY

Different individuals of *Anax junius*, a common North American species, and different parts of the same individual grow at different rates. This renders an *exact* definition of

the characteristics of any one of the thirteen larval instars impossible. Nevertheless it is believed that the age of a given larva may be determined within an approximation of one or two instars. All possible characters should be taken into consideration in making such determinations.

Many external structural and color changes during larval development of *junius* are described. Among those here announced for the first time are: alteration in position and extent of the moulting fissures, the striæ on the frons in the earliest instars, the formation and increasing depth of the secondary ligular cleft, the number of the teeth on either side of this cleft, the change in shape of the proximal segment of the labial palp, the correspondence of certain abdominal markings with internal points of attachments of muscles.

Similar studies of the last eight instars of *A. amazili*, a tropical American species, have been made and the results compared with those obtained for *junius* and the latter with those given by European authors for *A. imperator* and *A. parthenope*. What are believed to be the last exuviae of *A. longipes* are described from Pennsylvania and Florida; they are different from the larva previously considered to be this species. A larva from Borneo, probably *A. guttatus*, is also discussed.

The taxonomic characters of the larvæ of *Anax* are enumerated with special reference to those which are visible from the beginning of larval life; one of the chief of these is the presence of lateral spines on abdominal segments 7, 8 and 9 only.

A new synopsis of the larvæ and exuviae of the last pre-imaginal instar of nine species of *Anax* is given, primarily based on the principle of the biogenetic law: those species whose labial palps retain the truncated apex to the proximal segment being considered older phylogenetically than those in which this apex has ontogenetically become hooked; similarly, the deeper secondary ligular cleft is phylogenetically younger because ontogenetically late.

The breeding data and those on seasonal distribution of

A. junius are interpreted to mean that in most of North America two successive generations within a year do not occur; that under continued high temperature of both water and air two generations per year may be possible; that in any one permanent body of water, otherwise suitable, there will be found on any one day, larvæ of many different instars. Data on nine other species of *Anax* from different parts of the world are assembled and observations are suggested to determine whether they show similar seasonal distribution to that of *junius*.

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EXPLANATION OF THE PLATES

PLATE I

FIGS. 1-14. *Anax junius*.

FIGS. 1, 2. Dorsal views of head of 1st and 2nd instars respectively, 1 from Cheyney, Penna.; Oct. 7-10, 1929, 2 from Primos, Penna., Aug. 5-10, 1926. Small circles ooo seta pores from exuvia 1 and 2 of larva no. 3 respectively, xxx additional seta pores from exuvia 2 of larva no. 4 (Primos); ---, hind margin of brain, - - - -, moulting fissures. Fig. 1 shows also the frontal striæ, the cuticular denticles, arranged in rows, and the white cross-shaped mark.

FIGS. 3-5. Dorsal views of meso- and metathorax showing wing rudiments: 3 sixth instar, larva 210, 4 seventh instar, larva 208, 5 eighth instar, larva 204, all three

from Cheyney, Penna., Oct. 7 and 10, 1929. DC and VC become respectively the dorsal and ventral costal margins of the wing of the imago.

FIGS. 6-12. One-half of median distal mental margin of labium of the 1st to 7th instars respectively, 6 from a larva, May, 1918, from Prof. A. D. Whedon, 7-12 from exuviae of larva no. 3, Primos, Penna. In the eighth and following exuvial labia of no. 3 the small lateral tooth shown on the mental margin of fig. 12 has disappeared. PF primary and SF secondary ligular fissures.

FIG. 12R. Median mental margin of a larva just before the ninth moult, showing the new mentum, M', of the tenth instar cleft to proximad of the primary ligular fissure, PF.

FIG. 13. Median mental margin of last (13th) exuvia of larva no. 3, ventral view.

FIG. 14. Secondary ligular fissure of fig. 13, more highly magnified and without the setae.

FIGS. 15-16. *Anax guttatus?*, last larval instar, Borneo. Similar to figs. 13 and 14.

FIGS. 17-18. *Anax imperator*, last exuvia b, Indre, France. Similar to figs. 13 and 14.

FIGS. 19-23. *Anax amazili*, 19-20 last exuvia, Manaus, Brazil, June 20, 1922, similar to figs. 13 and 14. 21 Dorsal view of one-half distal median mental margin, larva a, probably sixth instar, S. Isidro de Cartago, Costa Rica, Sept. 20, 1909. 22-23 Last exuvia of larva no. 25, S. Isidro de Cartago, Sept. 1909, similar to figs. 13 and 14.

FIGS. 24-25. *Anax longipes*, last exuvia, Primos, Penna., Aug. 7, 1925. Similar to figs. 13 and 14.

FIGS. 13, 15, 17, 19, 22 and 24 are drawn to the same scale, shown on fig. 19.

FIGS. 14, 16, 18, 20, 23 and 25 are drawn to the same scale shown on fig. 14.

All the figures are camera lucida drawings by the author, using Zeiss compound microscope, oculars 2 or 4, objectives A (with or without its lower lens), C or DD.

PLATE II

FIGS. 26-28. *Anax junius*. 26 Anterior end of egg showing micropyle and surface reticulation, Ithaca, New York, Aug. 11, 1917; drawing by Prof. C. H. Kennedy. 27 Right labial palp of 1st, 3rd, 5th, 7th, 9th, 11th and 13th exuviae of larva no. 3 from Primos, Penna.; the figures 5, 7, 9, 11, 13 are placed on the "end hook." 28 Right labial palp of 1st exuvia of the same, more highly magnified, the single dorsal seta added from a larva from Prof. A. D. Whedon.

FIGS. 29-34. Right labial palps.

FIG. 29. *Anax guttatus?* larva, Borneo.

FIGS. 30-32. *Anax amazili*. 30 Larva a, probably 6th instar, S. Isidro de Cartago, Costa Rica, Sept. 20, 1909. 31 Last exuvia of larva no. 41, Cartago, C.R., Dec. 25, 1909. 32 Last exuvia, Manaus, Brazil, June 20, 1922; the indentation on the upper margin of the end hook near the external distal angle is a little exaggerated and is not a constant feature of the exuviae from Manaus.

FIG. 33. *Anax imperator*, last exuvia b, Indre, France.

FIG. 34. *Anax longipes*, last exuvia, Primos, Penna., Aug. 7, 1925.

FIGS. 35-39. Dorsal views of apex of male abdomen, last exuviae. C cercoid, IF inferior appendage (cercus), M median (dorsal) appendage, ♂ male projection.

FIG. 35. *A. junius*, larva no. 3, Primos, Penna. The apex of the male projection is often more concave in other individuals.

FIG. 36. *A. imperator*, d, Indre, France.

FIG. 37. *A. amazili?*, Manaus, Brazil, June 20, 1922.

FIG. 38. *A. amazili* no. 25, Cartago, Costa Rica, Sept., 1909.

FIG. 39. *A. longipes*, Primos, Penna., Aug. 7, 1925.

PLATE III

Anax junius, Smithson's Pond, Cheyney, Penna., Aug. 18, 1930. Instars probably as follows:

- FIG. 40. No. 230 7th instar ♂, "belted."
 FIG. 41. No. 234 8th instar ♀, not "belted."
 FIG. 42. No. 235 8th instar ♀, "belted."
 FIG. 43. No. 243 9th instar ♂.
 FIG. 44. No. 226 10th instar ♂.
 FIG. 45. No. 224 11th instar ♂.
 FIG. 46. No. 285 12th instar ♀.

A millimeter scale is placed below each row of figures.

PLATE IV

Anax amazili, Cartago, Costa Rica.

FIGS. 47, 48. Two views of larva *d* ♂, Aug. 22, 1909, probably octavult, or sixth, instar.

FIGS. 49, 50. Two views of larva *g* ♀, Oct. 25-27, 1909, probably quintult, or ninth, instar.

A millimeter scale is placed alongside each photograph.

The photographs for Plates III and IV were made by Mr. A. P. Apgar, Medical School, University of Pennsylvania, under a grant to the author from the Faculty Research Committee of the University.

The following corrections should be made in the author's paper of 1929, published in these *Proceedings*, volume 68, No. 3:

Page 240, Table 2, for 1926 read 1927.

" 252, line 18, for 1.26 read 1.28.

" " " 19, for five read nine.

" 266, insert Fig. 5 under figure.

" 270, 5th line from bottom, delete 1929.

PLATE I

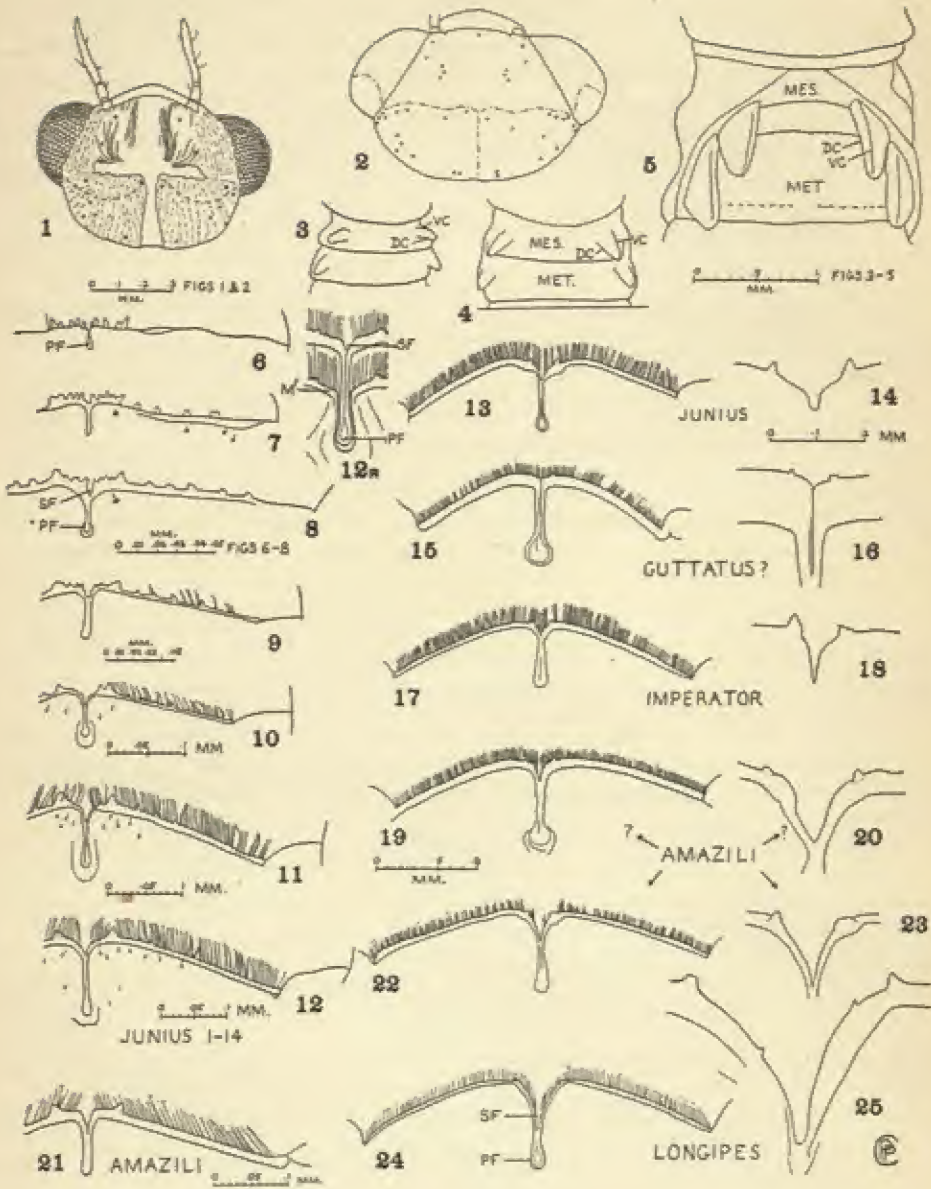
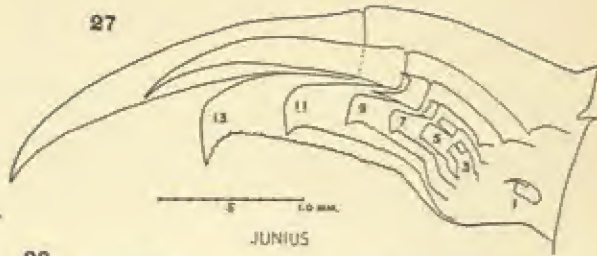


PLATE II



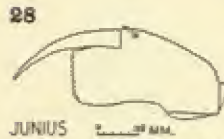
JUNIUS



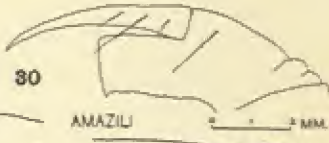
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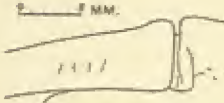
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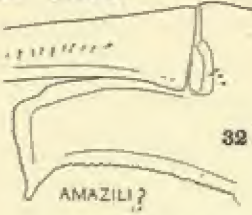
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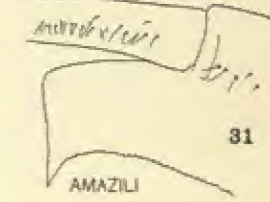
AMAZILI



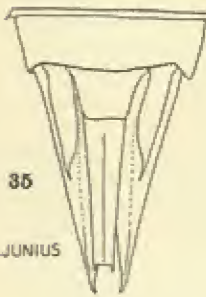
IMPERATOR



AMAZILI?

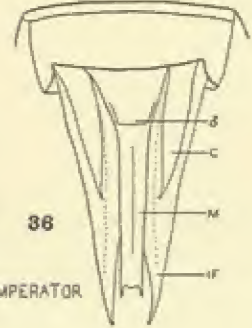


AMAZILI



35

JUNIUS



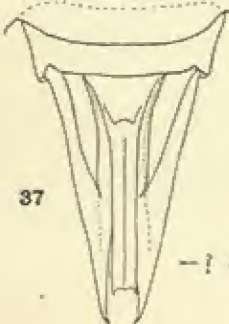
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IMPERATOR



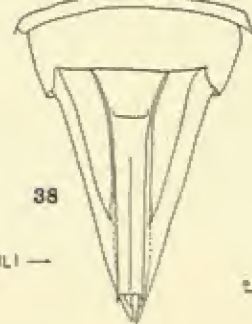
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LONGIPES

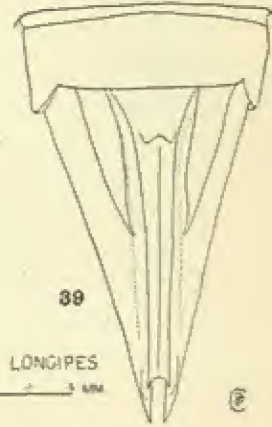


37

--? AMAZILI--



38



39

LONGIPES

PLATE III

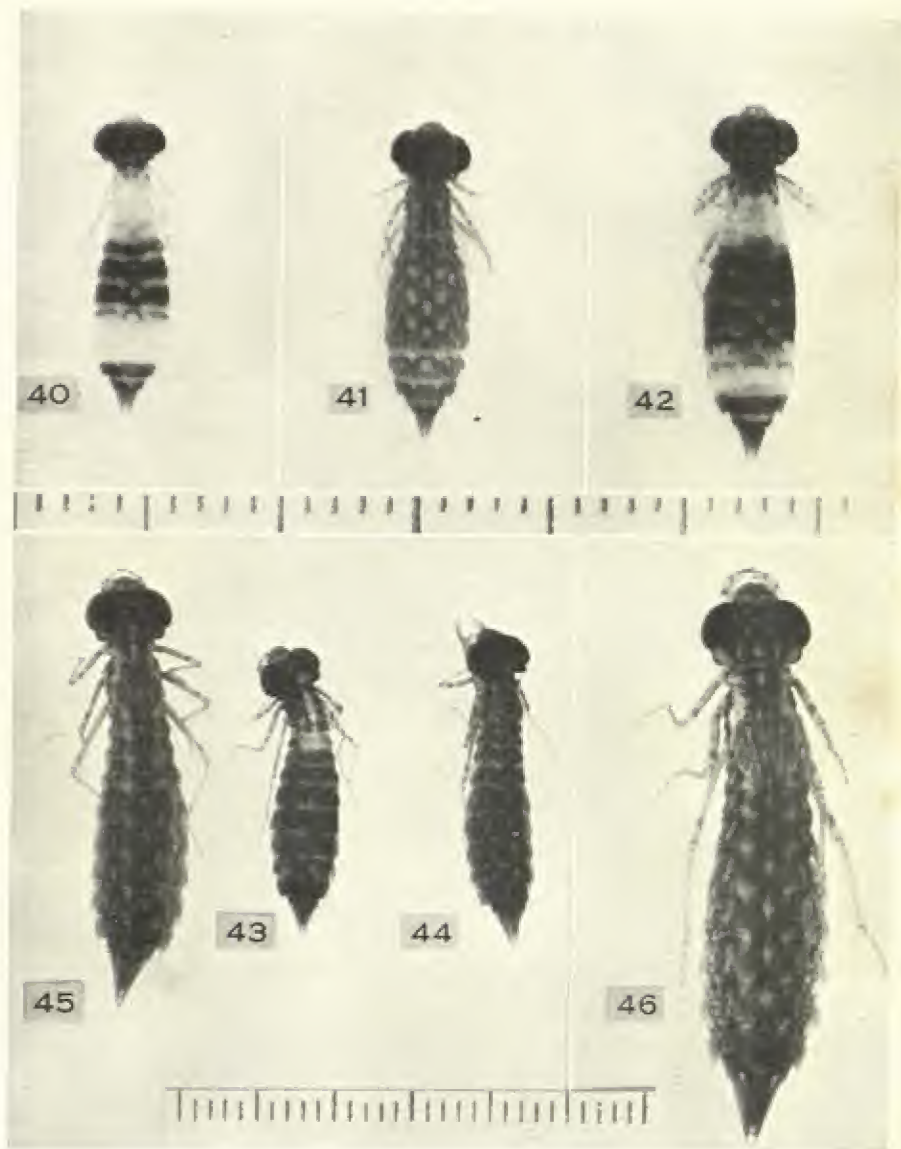


PLATE IV





A CONTRIBUTION TO THE OSTEOLOGY OF *TITANOIDES*
AND THE RELATIONSHIPS OF THE AMBLYPODA

BRYAN PATTERSON

A WELL preserved mandible of the rare amblypod *Titanoides* was presented to Field Museum by Mr. Edwin B. Faber of Grand Junction, Colorado, in 1931. This specimen was collected by its donor in Plateau Valley, Mesa County, Colorado, a locality from which fossil vertebrates had never before been reported. The jaw was the most complete specimen of the genus found up to that time and represented a new species. A description of this specimen, prepared by the present writer during the past year, has been recently published (Patterson 1933). As a result of the interest aroused in the Museum by this find a party consisting of Mr. T. J. Newbill, Jr., and the writer was sent out to make a preliminary reconnaissance of the type locality. Mr. Faber very kindly gave every assistance and pointed out remains of three individuals which he had discovered but had not attempted to take out of the ground; from one of these the holotype mandible, P 14637, had weathered out. In some six weeks of collecting four specimens of *Titanoides* (listed below), fragmentary crocodilian and turtle remains, two teeth of a tæniodont and a few invertebrates were secured (see p. 97).

The present communication is devoted to a preliminary description of the *Titanoides* material. The discovery that this genus is a large, graviportal pantolambdid with important tendencies toward the coryphodont type of foot structure was as unexpected as it was welcome. Further collecting at this new locality will be carried on during the coming season. Acknowledgments are due to Mr. Faber for his kind coöperation and aid, to Mr. Newbill for his zealous services and for the use of his automobile throughout the trip and to Mr. J. Elvin Harris of Mesa, Colo., and Mr. H. L. Wohlfort of Grand Junc-



tion for courtesies and assistance in the work. Much of the preparation has been skillfully done by Mr. J. B. Abbott. The drawings are by Mr. Carl F. Gronemann, Staff Artist, Field Museum, and the photographs by Mr. C. H. Carpenter.

Order AMBLYPODA Cope

Family *Pantolambdidæ* Cope

Titanoides may be referred with confidence to this family. The cranial and dental characters and many features of the limb bones, particularly the humerus, clearly indicate that it is a pantolambdid. The manus, however, shows an approach to that of *Coryphodon*. The tarsus is of the coryphodont type, particularly the astragalus which retains only a vestige of a neck and has a large, relatively flat, tibial facet closely approaching the navicular facet. One of the principal characters cited by Cope (1883, p. 406) as separating his suborders Taligrada (including the *Pantolambdidæ*) and Pantodonta (*Coryphodontidæ*) was the fact that in the former the head of the astragalus is distinct from the trochlea, whereas in the latter there is no head. *Titanoides* combines characters of both families and in referring it to the *Pantolambdidæ* some qualifications are necessary. The most practical arrangement in the present state of knowledge seems to be the erection of two subfamilies. The *Pantolambdinæ* may be defined as: Ambulatory pantolambdids of small size; tuber calcis of calcaneum relatively long; astragalus with distinct neck, tibial facet limited in extent and well separated from the navicular facet. The second group may be diagnosed as follows:

Titanoidinæ subfam. nov.

Large, graviportal pantolambdids; tuber calcis relatively short, heavy; astragalus with only a vestige of the neck, tibial facet large, facing vertically and approaching navicular facet.

Genus *Titanoides* Gidley 1917

The characters of this genus, so far as they are known at present, may be very briefly summarized as follows: Dentition

complete, canines moderately enlarged. Molars of pantolambdid type; upper M with proto- and metaconules either small or lacking, M^2 , M^3 strongly indented on the posterior margin; lower M with relatively strong paraconids and cristæ obliquæ; skull typically pantolambdid. Mandibular symphysis sloping, slightly recurved ventrally; articular surface of condyle elongate, facing both dorsally and posteriorly. Manus large, intermediate in structure between *Pantolambda* and *Coryphodon*; a centrale probably present; metacarpals and proximal phalanges similar to those of *Coryphodon*; unguals strongly fissured; tarsus close to the coryphodont type.

Titanoides faberi Patterson 1933

T. faberi Patterson 1933, *Amer. Journ. Sci.*, (5), 25, 417.
Horizon: Upper Paleocene (see p. 97).

The description given in this paper has been taken from the following specimens:

P 14637, holotype—an immature individual. Incomplete and distorted skull and mandibles, various vertebræ.

P 14902—a large fully adult animal. Complete mandibles, cervical series lacking atlas, various other vertebræ, chevron, ribs, clavicle, left scapula, more or less complete left fore leg and foot, fragmentary pelvis, patella.

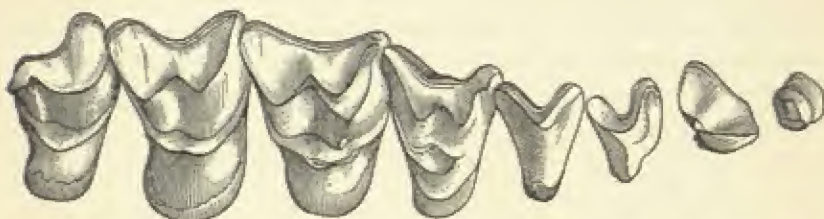
P 14904. Right tibia, fibula and patella of an adult specimen.

P 14908. Incomplete mandibles, various vertebræ, fragmentary pelvis, incomplete left hind leg and foot, various other bones not yet prepared. The remains are those of an immature individual and are in a very poor state of preservation.

The above are all from the same level and were found within a distance of a mile and a half; all are undoubtedly referable to the same species. They indicate an animal but little smaller than *Uintatherium* with a variation in size within the species of about 13 per cent.

Upper Dentition (Fig. 1, Pl. I).—In the holotype skull the milk canine, P^1 , dm^2-4 and M^1-3 are preserved. The crowns of the permanent premolars may be observed beneath

the milk molars. The milk canine is a very small, much abraded tooth. P^1 is set obliquely to the long axis of the tooth row; its structure is simple and consists chiefly of a stout, pointed central cusp, the parametacone, from the apex of which two crests extend antero-internally and postero-externally. The anterior, and shorter, of the two crests terminates in a small parastyle, the metastyle is not distinct; both



TEXT-FIG. 1. *Titanoides faberi*. Right milk canine, P^1 , dm^2 - dm^4 , M^2 - M^4 . Holotype, P 14637. $\times 34$.

crests are crenulated in the upper halves of their lengths. There are slight external and internal cingula, the external discontinuous. The internal cingulum is considerably thickened just posterior to the base of the parametacone. This thickening probably represents the beginning of the protocone.

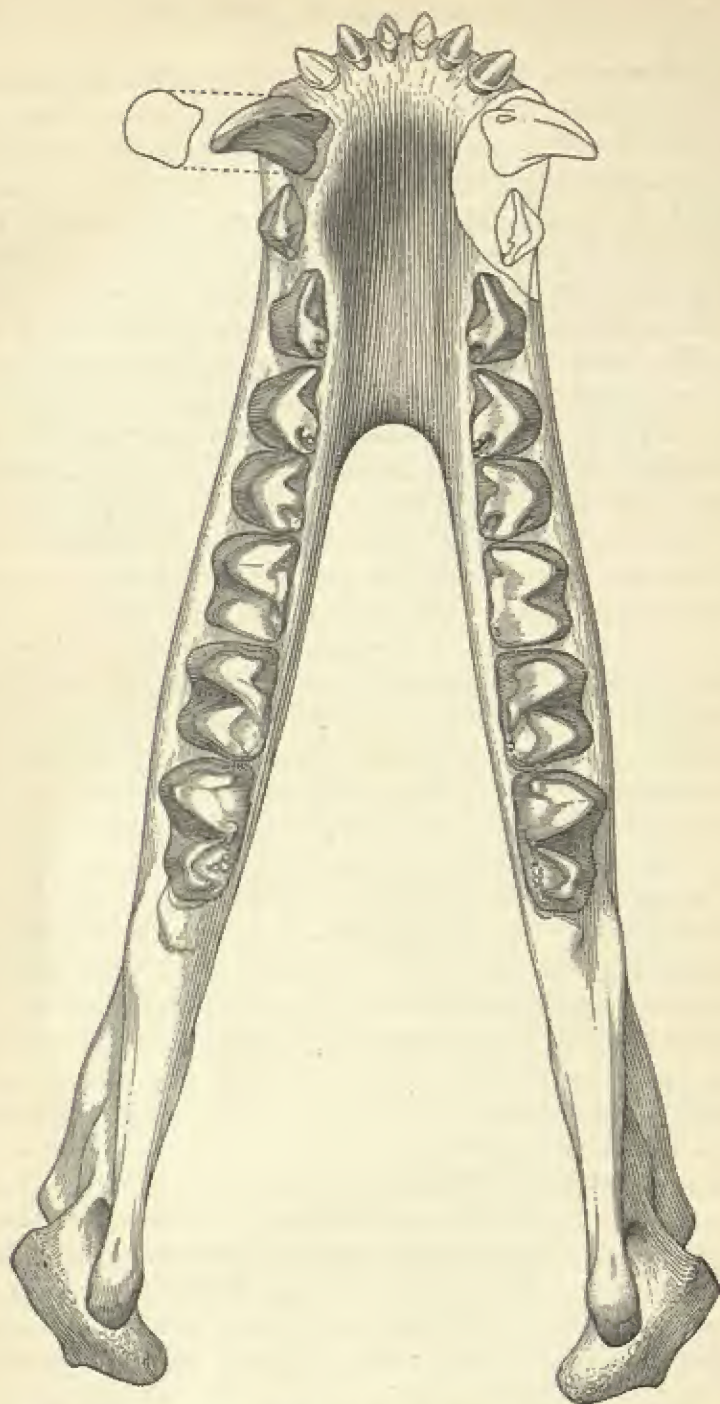
The milk molars are much abraded but nevertheless show features of considerable structural interest. Dm^2 is a small, triangular tooth with prominent and well separated parastyle and metastyle, conspicuous external cingulum, a central parametacone and an internal protocone. The latter is placed postero-internally to the parametacone and occupies very nearly the same position as the thickened portion of the internal cingulum of P^1 . Dm^3 is wider transversely than the preceding tooth, due to the larger size of the protocone, but is essentially similar in other respects. The fourth milk molar is much the largest of the series, being but little smaller than M^1 which it resembles fairly closely. The most important departure from the structure of dm^2 and dm^3 lies in the separation of the paracone and metacone which are divergent,

although not to such an extent as on the permanent molars. There is a small cusplular elevation on the external cingulum just opposite the newly formed mesostyle. The transition from parametacone to separated paracone and metacone shown in the deciduous teeth is striking and is in welcome and complete accord with current interpretations of the homologies of the coryphodont and pantolambdid upper premolars.

The upper molars are decidedly pantolambdid in pattern. M^1 differs from the corresponding tooth of *Pantolambda* in its slightly greater width, more prominent parastyle and incipient proto- and metaconule. In addition the internal cingula are represented only by slight crenulations on the anterior slope of the protocone. A small cuspule is present on both first molars at the base of the internal slope of the paracone. M^2 of *Titanoides* is considerably wider proportionately than that of the Torrejon genus. All traces of the proto- and metaconule are lacking. There is a continuous, crenulated internal basal cingulum which is indistinct around the internal slope of the protocone but becomes prominent at the base of the posterior slope. The outline of the tooth is considerably indented on the posterior face, a feature which imparts to it a curved appearance. As in *Pantolambda*, M^3 is a rather narrow tooth with a large paracone and parastyle and much smaller metacone and metastyle. It resembles the preceding molar and differs from the last named genus in the continuous internal cingulum and posterior indentation. The unworn cutting edges are crenulated throughout the molar series.

The isolated and fragmentary upper molar previously figured and described by the writer (1933, p. 422 fig. 4) and tentatively assigned to *T. faberi* is now shown to have been correctly referred.

Lower Dentition (Figs. 2, 3).—All the permanent teeth are represented, on one side or the other, in the mandible of P 14902. The small incisors increase in size from I_1 to I_3 , and are regularly spaced; the structure is essentially the same in each and consists of a single stout cusp, convex on the external face and slightly keeled with lateral concavities on the internal face. The latter surface bears a rather deep groove,

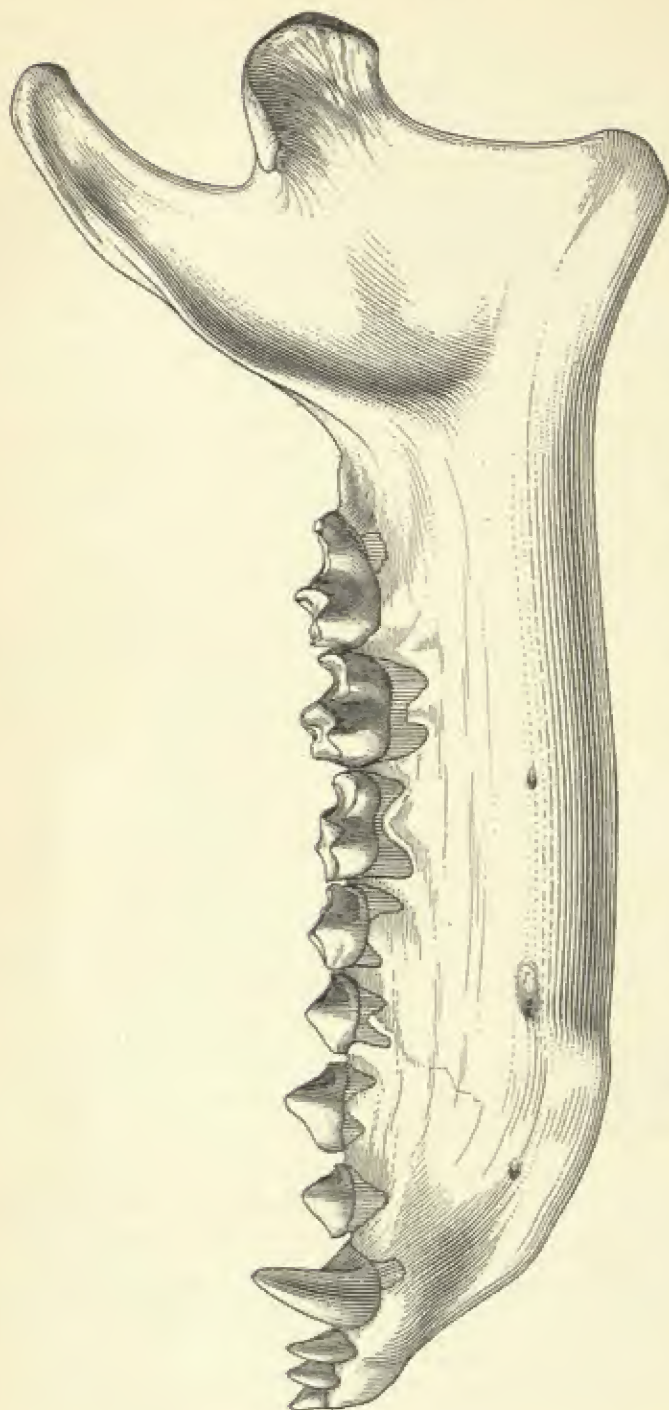


TEXT-FIG. 2. *Titanoides faberi*. Mandibles, dorsal view, P 14902. $\times \frac{1}{2}$.

parallel to the margin, at each side. There is no indication of the lateral cusps described by Jepsen in *T. gidleyi* (1930, pp. 506-507) although the areas demarcated by the lateral grooves in *T. faberi* are probably homologous with these cusps. A slight internal basal cingulum is present. The roots are long and slightly curved posteriorly. In view of the unworn condition of the incisors it seems likely that they were the last of the permanent teeth to erupt. The incisor roots of the holotype, P 14637, described earlier by the writer are therefore very probably of the deciduous series. The canine is large and robust with a prominent antero-internal style connected by a ridge to the apex of the tooth. The cross section of the crown is peculiar and is shown in text-fig. 2.

The Premolars.— P_1 is the smallest of the series, the remaining teeth are of approximately the same antero-posterior diameter, but increase in transverse diameter from P_3 to P_4 . The first has already been fully described and the additional material reveals nothing new. On P_3 the paraconid is larger and slightly more internal in position and the metaconid and talonid have increased in size. Small cuspules are present on the floor of the incipient talonid basin of this and the succeeding tooth. P_3 has a more internal paraconid and a larger metaconid than P_2 . The fourth premolar has been described previously; the trigonid in this tooth is essentially molariform although the paraconid and metaconid are not as high as those of the molars. The premolars illustrate in a satisfactory manner the development of the amblypod trigonid through the swinging in of the paraconid wing and the internal enlargement of the metaconid. They fail, however, to do the same for the talonid which remains low and inconspicuous throughout the series. The posterior basal cusp is presumably the hypoconid but there is trace of the entoconid. There is no evidence that this cusp has sprung, as it does in notoungulates, from one of the cuspules mentioned above for these continue in the molars.¹ The more important features of the

¹ These cuspules occur in the holotype mandible. They were not mentioned in the original description as it was thought that they might be an individual peculiarity. Their presence in P 14902, however, shows that they may be considered as an additional specific character for *T. faberi*.



TEXT-FIG. 3. *Titanoides faberi*. Left mandible, side view, P 14902. $\times \frac{1}{2}$.

molars have already been described. The incipient metastylid present on M_3 of the holotype is also found on the same tooth of P 14902. The entoconid on all teeth of the series sends a spur internally.¹ There is a basal cingulum on the internal half of the posterior side of each molar, this cingulum becomes cuspidate on M_3 . The cuspules in the talonid basin of this tooth are numerous and fairly well developed.

The skull (pls. I, II) of the immature holotype is, unfortunately, very badly crushed and distorted thus rendering it impossible to give more than a cursory account of the principle features.

The rostral portions of the premaxillaries are missing, the ascending rami reach the nasals. The latter are long and smooth, extend between the orbits and are somewhat expanded posteriorly. The anterior nares are terminal, the zygomatic arches slender and the post-orbital processes of the frontals incipient. The anterior border of the orbit is over dm^4 . The side walls of the posterior nares are greatly extended backwards as in *Pantolambda* (Osborn and Earle, 1895, p. 46). The post-glenoid processes of the squamosals are considerably produced ventrally, narrow antero-posteriorly and have a fairly extensive articular surface on the anterior face. The mastoid processes are extremely prominent and robust; they form the ventral border of the posterior wall of the widely open auditory channel.² There is a sagittal crest but this is not very prominent; an older specimen would probably show a greater development of this structure.

A comparison of the characters listed above with those given by Osborn (1898b, pp. 177, 184) for *Pantolambda* clearly indicates the fundamental similarity between the skulls of the two genera. There is no feature in the skull or dentition of

¹ The entoconid 2 of Osborn (1898b, p. 173).

² The writer feels that this term, or some other comparable to it, is better employed in cases in which a bony floor of the auditory opening is unknown or definitely known to be absent. The term meatus should be restricted to cases in which the opening is closed ventrally for all or nearly all of its length either by union of the post-glenoid process of the squamosal with the post-tympanic process (meatus spurius), or by the

Titanoides which is not of the pantolambdid type or which approaches *Coryphodon* in any significant manner.

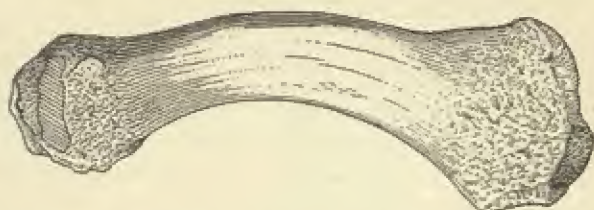
The Mandible (Figs. 2, 3).—The symphysis and horizontal ramus of the lower jaw of P 14902, although larger, are essentially similar to those of the holotype P 14637 (Patterson, 1933, p. 421). The posterior mental foramen in P 14902 is beneath $P_{\frac{3}{8}}$ rather than beneath $P_{\frac{1}{4}}$ as it is in the holotype. The post-dental portion of the jaw is less robust than that of other amblypods and has a rather superficial resemblance to the corresponding region of the uinatheres. The coronoid process is slender, fairly high, and curved backward; the supracondylar notch is wide and prominent. The condyle is low, being placed just above the level of the cheek teeth, and set on a distinct neck. The articular area is elongate and faces both dorsally and posteriorly; the dorsal portion is narrow and runs obliquely in a postero-internal direction, the posterior portion is wider and faces directly backwards to articulate with the deep post-glenoid process of the squamosal. This extensive articulation, permitting great freedom of movement of the mandible, is paralleled by several forms, notably *Homalodontotherium* and *Notharctus crassus*. The available figures of *Coryphodon*, *Pantolambda* and the *Dinocerata* do not show a comparable development. The angle is rather sharp and extends downward below the level of the inferior border of the horizontal ramus; the subcondylar notch is slight. The masseteric fossa is well marked but the pterygoid fossa is very poorly defined; the dental foramen is small and situated rather far back.

Description of the *vertebrae* is reserved for the present but a few general statements may be made here. The spine of the axis is very similar to that of *Coryphodon*; the size of the *vertebrae*, as in *Pantolambda*, increases considerably towards the posterior dorsals and lumbar. The centra are biconcave as in other amblypods. The anterior caudals, as indicated by one associated with P 14902, are extremely large. The cen-

tympanic (true cylindrical meatus). Such distinctions may appear rather fine but they are nonetheless of importance in exact work on the auditory region. For a review of meatus structure see Van der Klaauw, *Bull. Amer. Mus. Nat. Hist.*, 62, 137-157, 1931.

trum of this vertebra has a diameter of over 70 mm. and bears hypapophyses on the underside. With the same specimen is a bone that can only be interpreted as a chevron.

Among the bones comprising P 14902, is one which is identified as a *clavicle* (fig. 4). The shaft is irregularly pear-

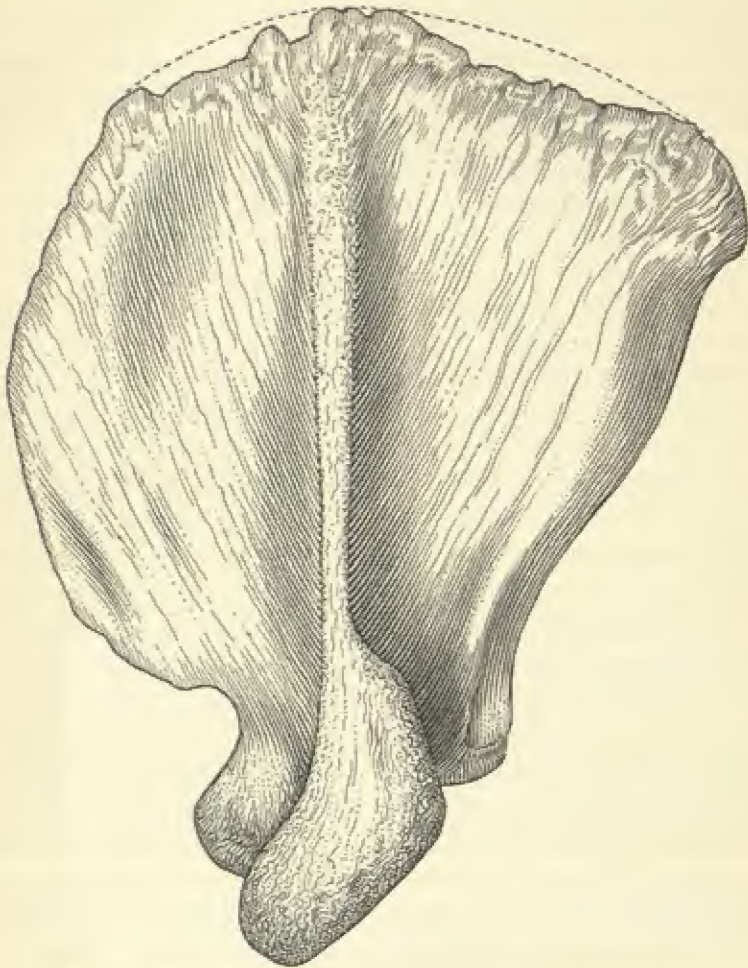


TEXT-FIG. 4. *Titanoides faberi*. Clavicle, P 14902. $\times 1/3$.

shaped in cross section and quite strongly arched. The ends are very dissimilar, one is flat and considerably expanded, the other more rounded with a rugose extremity. No definite articular surface is visible either on this supposed clavicle or on the acromion process of the scapula. The articulation with the scapula may have been cartilaginous, as it is in many living forms. No clavicle has been reported in *Pantolambda*. Cope (1877, 193-194) described some slender bones which he regarded as clavicles of *Coryphodon*. Marsh (1893, p. 325) denied their presence in this genus and Osborn (1898a) makes no mention of them. The presence in *Titanoides* of a bone which appears to be a clavicle renders it probable that Cope may have been right. The small bones which he described, if clavicles, possibly had no direct connection with the sternum or scapula but may have been joined by cartilage. No clavicles have been found with any uintathere and, in view of the comparatively small acromion of these forms, it is practically certain that they were lacking.

The *scapula* (fig. 5) is large and broad, almost as broad as it is long, and suboval in outline. The suprascapular border is gently arched and there is no angle between it and the comparatively thin coracoid border. The glenoid surface is considerably thickened and bears a prominent keel along the

edge of the bone. The coracoid process is large and stout, the coraco-scapular notch is wide, and deeper than the same in *Coryphodon*. The spine arises very close to the suprascapular



TEXT-FIG. 5. *Titanoides faberi*. Left scapula, P 14902. $\times 1/4$.

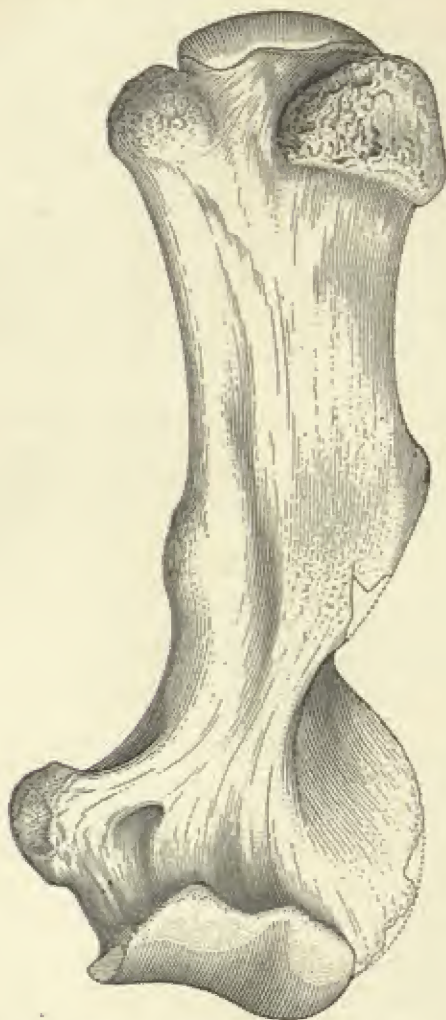
border, gradually increases in height and decreases in width toward the acromion process. The latter expands somewhat posteriorly; the broad, thick and rugose main portion turns anteriorly to extend down beyond the coracoid process which

it partly overhangs. The supraspinatus and infraspinatus fossæ are approximately equal in area although of somewhat different shapes. The scapula of *Pantolambda* is unknown. It has been restored by Osborn (1898b, p. 183, fig. 9) after that of *Coryphodon*. It seems probable, in view of the many fundamental resemblances between the osteology of *Pantolambda* and *Titanoides*, that it would resemble that of the latter. Between the scapulæ of *Titanoides* and *Coryphodon* there are several striking differences. The two genera, however, appear to have more important characters in common, such as the approximately equal supra- and infraspinatus fossæ, large acromion process and lack of any very noticeable angle between coracoid and suprascapular borders, than either has with the Dinocerata. The amblypod scapula is not of the extreme graviportal type.

The *humerus* (fig. 6) is long, massive and of a primitive type; the specimen at hand is flattened to some extent but the principal features are clear. The head is large, circular and in this specimen faces posteriorly and a little dorsally. The tuberosities are very large, face anteriorly and are separated from the head by well marked grooves; the bicipital groove is extremely deep. The deltoid crest is long and prominent. The distal end of the bone is considerably wider than the proximal. The supinator crest is thick and flaring, the entocondyle is very large and there is a large entepicondylar foramen. The distal articular surface is set rather obliquely to the long axis of the bone; the capitellum is rounded. The humeri of *Titanoides* and *Pantolambda* are fundamentally similar. The tuberosities in the former genus are a trifle more prominent, the bicipital groove is deeper and the ectepicondylar crest stronger, the last being a graviportal character. These characters in both genera differ somewhat from those in *Coryphodon*. The lesser tuberosity and the entocondyle of the latter are smaller and there is no entepicondylar foramen.

The *radius* (fig. 7) is a stout, outwardly curving bone. It is somewhat shorter than the humerus but the disparity in size between the two is not as great as it is in *Pantolambda*

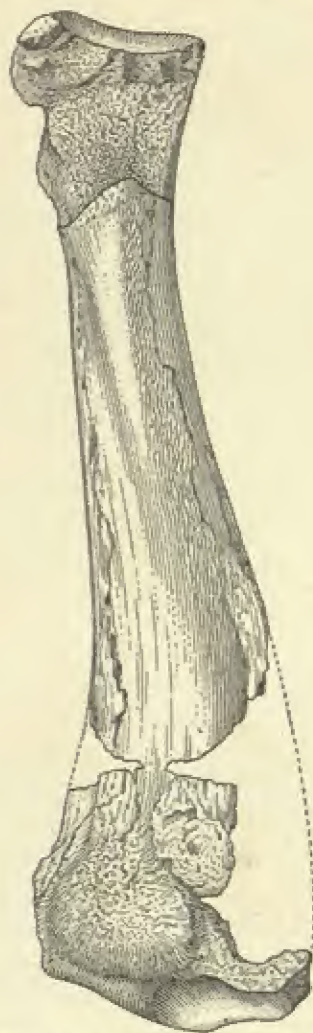
(see p. 93). The bicipital tuberosity is large. The shaft is roughly triangular just below the tuberosity but from this point down it becomes flattened antero-posteriorly and in-



TEXT-FIG. 6. *Titanoides faberi*. Left humerus, P 14902. $\times 1/4$.

creases in width transversely. The posterior face of the distal half of the shaft is concave. The distal end is very wide and is extremely rugose just above the articular surfaces.

The facet for the scaphoid is oval in outline, concave and separated from the lunar facet by a very prominent keel. Only the proximal third of the *ulna* (fig. 8) is preserved. The

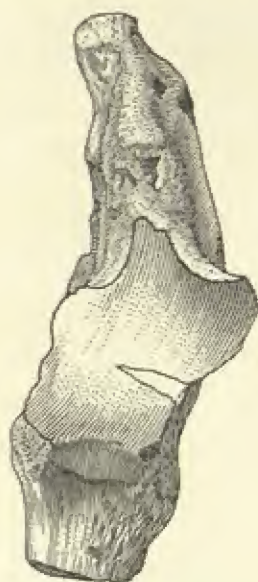


TEXT-FIG. 7. *Titanoides faberi*. Left radius, P 14902. $\times 1/3$.

olecranon is very rugose, laterally compressed and curved outwardly. It is considerably wider antero-posteriorly than that of *Coryphodon*. The great sigmoid notch in *Titanoides* is

about as deep as in the last named genus and is much shallower than in *Pantolambda*.

The *manus* (fig. 9) is larger and relatively broader than in *Coryphodon*. The distal row of carpals is preserved. The unciform is extremely large, articulates, as in other ambly-



TEXT-FIG. 8. *Titanoides faberi*. Proximal end of left ulna, P 14902. $\times 1/3$.

pods, with Mcs. III, IV and V, and has a slightly concave facet for the cuneiform. The facet for the lunar is distorted, increasing the height of the bone; this defect has not been corrected in the drawing. The magnum is structurally transitional between that of *Pantolambda* and that of *Coryphodon*. The distal end is considerably enlarged and has an extensive articulation with Mc. II, as in the latter genus, while the proximal end narrows towards the lunar facet, as in the former. A considerable space is thus left between the magnum and the trapezoid. It appears almost certain that this was filled by a centrale as in *Pantolambda*. The trapezoid is relatively large and resembles that of the last named genus in the contour of the articular surface for the scaphoid and (?)

centrale. It is, however, deeper and has a more sharply convex facet for Mc. II. The trapezium is a large bone and is expanded distally. As in the creodonts and the other



TEXT-FIG. 9. *Titanoides faberi*. Incomplete left manus, P. 14902. $\times 1/3$.

amblypods it rests upon Mc. I, articulates laterally with Mc. II and has a proximal facet for the scaphoid. The facet for the trapezoid is oblique. The metacarpals are stout broad bones similar to those of *Coryphodon* and very different from the more slender ones of *Pantolambda*. Mc. I articulates with the trapezium only and does not touch Mc. II; it is somewhat longer than in *Coryphodon* and extends distally below Mc. II. The lateral moieties of the proximal ends of Mcs. II and III are thrust up between the trapezoid, magnum and the unciform to a greater extent than is the case in either *Pantolambda* or *Coryphodon*. The proximal facet of Mc. V is long in the antero-posterior diameter

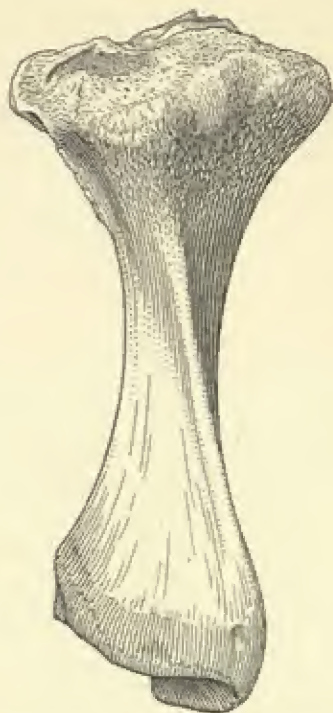
and was perhaps in contact posteriorly with the cuneiform, as in many specimens of *Coryphodon*. On the external side of the proximal end there is a large, rugose area, probably for the insertion of the extensor carpi ulnaris muscle. The first and second phalanges are almost identical with the corresponding bones of *Coryphodon*. The unguals, however, are unique. They are fairly long, broad, flattened and deeply fissured. Osborn (1898b, p. 184, fig. 10) has figured an ungual of *Pantolambda* which is cleft but this particular specimen appears to be the only one showing this peculiarity as the other and more complete specimens of this genus figured by the same writer show no trace of a fissure. Fissured unguals are characteristic of the inadapative creodonts; the presence of this feature in *Titanoides* is important in view of the many creodont characters which Osborn (1898b) has noted in the osteology of *Pantolambda*.

The manus of *Titanoides* is of exceptional interest both structurally and taxonomically. The metacarpals and proximal phalanges are of the coryphodont type. The probable presence of a centrale is a pantolambdid feature, the structure and relative sizes of the magnum and trapezoid are intermediate between the two. A little further reduction of the trapezoid and the enlargement of the proximal end of the magnum would transform the distal carpal row of this genus into one identical with that of *Coryphodon*. The foot has been drawn in a partially extended pose in which position it is sub-digitigrade; in maximum flexion, however, it is fully digitigrade.

The femur of P 14908 is so crushed and distorted that accurate description of it is impossible. The great trochanter is relatively larger than that of *Pantolambda*; the second, although broken, appears to have been small; the third trochanter is prominent and placed rather low on the shaft. The condyles are almost equal in size and are separated by a rather narrow intercondylar notch. The patella of P 14902 is large and broad. The articular surface is gently concave proximodistally and very slightly convex transversely.

The tibia and fibula are very short and stout. The proxi-

mal end of the *tibia* (fig. 10) is massive and rather more rectangular than trihedral in outline. The shaft is triangular in cross section at the middle. The spine is very small. The



TEXT-FIG. 10. *Titanoides faberi*. Right tibia, P 14904. $\times 1/3$.

external facet is broader in the transverse than in the antero-posterior diameter and is slightly higher than the internal. The latter is circular and is the more concave of the two. The prominent cnemial crest runs diagonally to merge with the internal malleolus, much as in *Pantolambda*, imparting a somewhat twisted appearance to the bone. The crest, thick and massive proximally, becomes thin and sharp at the middle of the shaft. The distal end of the bone is considerably wider transversely than antero-posteriorly. The internal malleolus is short but very thick; the articular surface for the side of the astragalus is decidedly convex antero-posteriorly. The artic-

ular surface for the dorsal face of the astragalus is set obliquely to the long axis of the shaft and is very gently convex in the transverse diameter. The entire distal articulation is very similar to that of a specimen of *Coryphodon* figured by Cope (1877, pl. 54, fig. 4). The tibia of *Titanoides* differs from that of *Pantolambda* and agrees with that of *Coryphodon* in its relative shortness. It resembles the former, however, and differs from the latter in the prominent cnemial crest.



TEXT-FIG. 11. *Titanoides faberi*. Right fibula, P 14904. $\times 1/3$.

The *fibula* (fig. 11) has a slender shaft, and is expanded at the proximal and distal ends. The proximal articular surface for the tibia is large, roughly circular and oblique to the long axis of the bone. The shaft is slightly bowed posteriorly and is lenticular in cross section. This outline is caused by two sharply defined ridges which have their inception at the proximal end of the bone in the center of the external and internal faces. From these points of origin the ridges run diagonally to the postero-external and antero-internal corners, respectively, of the distal end. The external malleolus is somewhat

compressed transversely, it is slightly wider at the anterior end than at the posterior. The articular surface for the tibia is small, the surface for the astragalus is large, convex proximally and concave distally. There is no articular surface for the calcaneum on either of the fibulæ at hand. It is possible, however, in view of the known variability of this feature in *Coryphodon*, that it may be found in other specimens. The fibula is very similar to that of a *Coryphodon* figured by Cope (1877, pl. 63, fig. 3).

The *pes* (fig. 12).—Bones of the hind foot were found in association with one specimen only—the immature P 14908.



TEXT-FIG. 12. *Titanoides faberi*. Incomplete left tarsus, P 14908. $\times \frac{3}{8}$.

Unfortunately these were greatly damaged by percolating water and the roots of plants. Despite their poor preservation, however, many important structural features can be determined.

The astragalus is a heavy bone of the coryphodont type, deeper at the distal extremity than at the proximal. It is somewhat weathered on the internal side. The facet for the fibula is irregularly rectangular in outline, convex antero-posteriorly and slightly concave dorso-ventrally. The facet for the internal malleolus is largely broken away. The dorsal

facet for the tibia is large and gently concave in the transverse diameter; it faces vertically and closely approaches the facet for the navicular. The latter is very deep dorso-ventrally and decidedly convex in that diameter. A shallow groove between this and the dorsal tibial facet is the only remnant of the neck. The articular surface for the cuboid is large and somewhat egg-shaped in outline. Of the two plantar facets for the calcaneum the ectal is the smaller and is relatively flat. The sustentacular facet is lower, longer and much more concave. The two are separated by a wide, deep groove which is closed proximally. A sharp ridge on the postero-internal corner of the bone terminates on the plantar surface in a prominent hook at the proximal end of the sustentacular facet. There is no trace of an astragular foramen. This structure is variable in *Coryphodon* and a larger series of *Titanoides* might contain individuals in which it was present. A feature of considerable interest in the astragalus at hand is the size of the angle between the planes of the navicular and tibial facets which, as accurately as can be determined from the specimen, is about 75° . Osborn (1898a, p. 89; 1929, p. 729) has given a series of sections of various astragali showing the angles between these two planes in plantigrade and digitigrade forms. The angle in the plantigrade *Pantolambda* is 83° and in the transitional *Coryphodon* 69° . *Titanoides* is thus intermediate between the two genera in this respect.

The Calcaneum.—The tubercalcis is short, deep and laterally compressed. The articular area for the astragalus is broadly quadrangular, more so than in the various calcanei of *Coryphodon* figured by Cope (1877, 1884), and somewhat emarginate proximally and distally. The two facets are separated by a shallow depression. The ectal is nearly plane and is the higher of the two. The sustentacular facet is gently convex, somewhat longer proximo-distally than the ectal and bears a fairly prominent lip formed by the projecting internal face of the bone. The articular surface for the cuboid is poorly preserved but enough of it remains to show that it faces obliquely in the internal direction and that it is smaller than the cuboidal

facet on the astragalus. The plantar surface of the calcaneum supports ridges on the external and internal borders, the internal ridge is shorter but much more prominent than the external. The navicular and the cuboid are preserved but present no very significant characters.

The available parts of the hind foot are strikingly similar to those of *Coryphodon*, much more so than is the case with those of the carpus. The short tuber calcis, the wide, vertically facing tibial facet of the astragalus and the close approach of the latter to the navicular facet are important resemblances to the Lower Eocene genus. If the pes of *Titanoides* had been found isolated in the matrix it would, without much question, have been referred to the Coryphodontidæ.

Limb Ratios.—The researches of Osborn and Gregory (see Osborn, 1929, chaps. IX and X) have thoroughly established the fact that with increase in size or of cursorial adaptations within phyla the limb proportions and many of the bones of the skeleton undergo considerable change in response to the trend followed. In graviportal adaptation the femur and humerus, and in some cases the radius as well, increase in length while the metatarsals and metacarpals shorten. In the following table the limb ratios of *T. faberi* are compared with those of two other amblypods and a Uintathere, the figures for which have been taken from Osborn. The measurements of the hind limb of *Titanoides* are from P 14908 and those of the fore limb from P 14902.

	Femur	Tibia	Tibio-femoral ratio	Mt. 3	Meta-tarso-femoral ratio	Humerus	Radius	Radio-humeral ratio	Mc. 3	Meta-carpo-humeral ratio
<i>Pantolambda bathmodon</i>	149	114	76	36	24	124	82	66	31	25
<i>Titanoides faberi</i>	403	300	74	75*	18	513	383	74	100	19
<i>Coryphodon lobatus</i>	423	260	61	62	14	363	240	66	70	19
<i>Uintatherium mirabile</i>	692	360	53†	70	10	540	380	70	106	19

* Only one metatarsal is preserved with P 14908 and this is quite probably not Mt. 3.

† Should be 52.

The ratios for the hind leg of *Titanoides* are, unfortunately, not accurate. The bones are considerably distorted, the femur appears to be shortened by compressure and the tibia elongated. Well preserved bones would probably give ratios closer to those of *Coryphodon*.

Titanoides is a graviportal form; in fore-limb proportions it is even more advanced than *Uintatherium mirabile*; in hind limb proportions it is, on the basis of the measurements of P 14908, intermediate between *Coryphodon* and *Pantolambda*. The structural advances of *Titanoides* over the last named form are apparently due to its larger size; such characters as the larger ectepicondylar crest, broader magnum and metacarpals, shorter tuber calcis and more compact astragalus are, to judge from analogous developments in the titanotheres, the direct result of the acquisition of graviportal proportions by members of this genus.

Relationships.—The several points of resemblance to *Coryphodon* in the limbs and feet of *Titanoides* are almost certainly habitus characters, results of the attainment by the genus of size and weight. The heritage characters indicate inclusion within the *Pantolambdidae*. The dentition (p. 73) and the skull (p. 79), parts of the skeleton not liable to much modification by increasing size and weight alone, are fundamentally similar to *Pantolambda*. The essentially primitive structure of the humerus and the stout cnemial crest of the tibia are pantolambdid features. The carpus (p. 86) has very evidently been derived from the pantolambdid type, as is evidenced by the transitional structure of the magnum and trapezoid; a centrale was probably present. Despite the many important characters in common between the two genera, however, and also the fact that one succeeds the other in time, it seems probable that *Pantolambda* was not ancestral to *Titanoides*. The writer has previously pointed out (1933, p. 423) that in certain features, such as the slightly larger paraconids, narrower talonids and more prominent cristæ obliquæ of the lower molars, the latter genus is more conserva-

tive than the former. The new material furnishes no evidence in disproof of this view and some points in favor of it. The absence or incipient condition of the proto- and metaconules in *Titanoides* is a primitive character. Fissured unguals are not characteristic of *Pantolambda* and their presence in *Titanoides* may perhaps be regarded as a primitive survival. The mandibles and the second and third upper molars of the latter are quite distinctive and probably not directly derivable from the Torrejon genus. As a final consideration it seems unlikely that the large, graviportal *Titanoides* could have evolved from the small, ambulatory *Pantolambda* between the middle and upper Paleocene. It is more probable that the two subfamilies diverged during early Paleocene time.

Titanoides cannot be considered as ancestral to *Coryphodon*. If the tarsal structure alone were known it might be so regarded but the skull and dentition definitely preclude close relationship. The two genera are nearly, perhaps exactly, contemporaneous (see p. 100) and it would appear impossible for the one to have been derived from the other in the time available. In fore-limb ratios *Titanoides* is the more advanced of the two.

Titanoides and the Amblypoda.—In order to bring out fully the important bearing of this genus upon amblypod classification a brief summary of the taxonomic history of the order may be given. Cope proposed three subordinal divisions, Taligrada (*Pantolambdidae*), Pantodonta (*Coryphodontidae*) and Dinocerata. Osborn and Earle (1895) suggested the addition of the Periptychidae to the Taligrada, a step which was taken by Cope (1897); Matthew (1897) retained this family in the Condylarthra but later (1928) included them in the Taligrada. Osborn (1898b) considered the three suborders as successive and broadly ancestral. The classification proposed by Cope has, in the main, been followed by most subsequent writers although some have suppressed the subordinal divisions and others have referred the periptychids to the Condylarthra. In recent years, however, as a result of careful work on the homologies of the molar teeth by H. E. Wood

(1923), Matthew (1928, pp. 969-970) and Simpson (1929b) it has become evident that the molars of the *Pantolambdidae* and *Coryphodontidae* have an entirely different developmental history from those of the *Dinocerata*. So considerable are the distinctions (see especially Simpson, 1929b) that it seems likely that the two groups would have been referred to separate orders had they been known from the teeth alone. The fact, however, seemed to contradict the evidence of the dentition. In foot structure the *Periptychidae* and *Pantolambda* are in close agreement; *Pantolambda* differs rather widely from the *Coryphodontidae* and the latter, in turn, resemble the *Dinocerata* very closely. So close, indeed, is the resemblance that Matthew (1928, p. 970), having the differences of the dentition in mind, wrote that "the close correspondence in the foot structure is hardly to be explained away as due to mere parallelism." Simpson in his recent classification of the mammals (1931) separated the *Amblypoda* (containing the *Periptychidae*, *Pantolambdidae* and *Coryphodontidae*) and the *Dinocerata* ordinally but emphasized the fact that the arrangement could not be regarded as definitive in the light of the evidence then available. He stated that "The arrangement of these diverse families is tentative at best. On the basis of the teeth a division into (1) *Periptychidae*, (2) *Pantolambdidae* and *Coryphodontidae*, and (3) *Uinatheriidae* would be possible. The feet would rather suggest a division into (1) *Periptychidae* and *Pantolambdidae*, and (2) *Coryphodontidae* and *Uinatheriidae*. . . . They seem to be diverse lines from the most ancient ungulate stock and their aggregation into higher than family units cannot yet be definitive."

The combination of characters exhibited by *Titanoides* to some extent clarifies this rather confused situation. It has long been recognized that *Pantolambda* is an ideal structural ancestor for *Coryphodon* as far as the dentition is concerned. The graviportal *Titanoides* supplies definite evidence tending to show that the *Coryphodon* foot has been evolved from the *pantolambdid* type as a result of increasing size and weight in the *coryphodont* phylum. The *Pantolambdidae* and *Cory-*

phodontidæ may now be regarded as constituting a natural group in foot structure as well as in the dentition. Recognition of this fact gives some support to Simpson's classification by increasing the probability that the resemblance in foot structure between the uintatheres and coryphodonts is due to parallelism despite the close structural similarity. This question is by no means settled but it seems preferable to the writer to regard the Dinocerata as distinct from the Amblypoda, at least until further evidence is forthcoming. Knowledge of the foot structure of the Paleocene Dinocerata is greatly to be desired in this connection.

The position of the periptychids, which resemble the Pantolambdinæ in foot structure but not in dentition, is rendered very uncertain by the new evidence. The order Amblypoda, as here understood, consists of the natural group Pantolambdidæ-Coryphodontidæ. The Periptychidæ may perhaps be regarded for the present as Amblypoda? inc. sed. together with the Tricuspidodontidæ. Little has been published on the family since Matthew's early memoir on the Puereco fauna and the latest and most authoritative views of that author are not yet available.

Geologic Horizon of T. faberi.—In the first paper on this species the writer tentatively concluded, on the basis of the distribution of the other two species of the genus, that it was from an upper Paleocene horizon (1933, pp. 424-425). This opinion has received some support from the work of the 1932 season. The turtle and crocodilian remains mentioned in the introduction are not yet available for study but the tæniodont teeth and the gastropods have furnished evidence of value. Dr. George Gaylord Simpson very kindly undertook to compare the tæniodont teeth with the abundant material in the American Museum and prepared the following statement.¹ "The rather uncharacteristic and variable patterns and the fact that the available specimens are either deeply worn or dissociated makes it difficult to establish homologies in this group, but the Ruby teeth are probably lower cheek teeth. They may be $P_{\frac{1}{4}}$ or $M_{\frac{3}{4}}$, as they have small entoconids,

¹ Letter to the writer May 16, 1933.

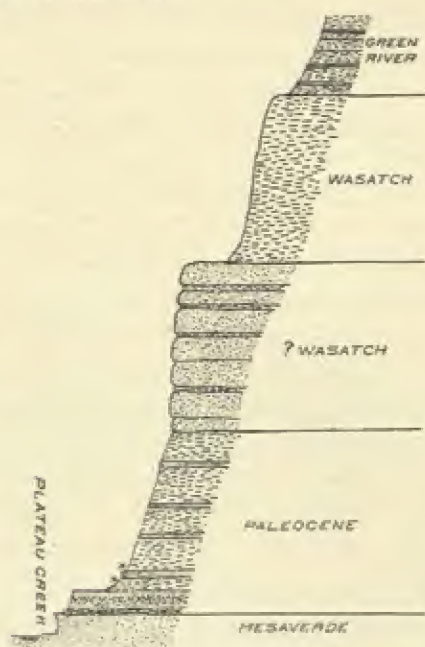
while those of M_{I-2} are relatively larger in *Psittacotherium* and *Calamodon*. The species is somewhat larger than *P. multifragum* and about the size of *C. simplex*. These teeth differ from *Psittacotherium* in the more completely united and more swollen roots, the apparent presence of cement on the roots, and the somewhat higher crowns. These are all advances in the direction of *Calamodon*, but the teeth differ from and are more primitive than *Calamodon* in their distinctly lower crowns. These characters suggest ?*Psittacotherium lobdelli* [see Simpson, 1929a, pp. 11-12], but as there are no homologous teeth direct comparison is impossible. The degree of evolutionary advance is about the same in the Ruby species and that from Bear Creek. If there is a difference, the Bear Creek species may be a little closer to *Psittacotherium* and that from the Ruby beds a little closer to *Calamodon*, but this is little more than a guess in view of the nature of the material.

"These teeth are inadequate to define the age of the beds in which they occur, but they are suggestive. Presupposing that they are normal, of a species neither precocious nor retarded in its evolution, one might establish a scale of probabilities. It is practically certain that their age lies in or between Middle Paleocene (Torrejon) and Lower Eocene ('Wasatch'). It is very probable that they are later than Torrejon and still probable, but with a little less security, that they are earlier than Gray Bull (or Sand Coulee). There is therefore some probability that they are of Tiffany or Clark Fork age, and of these two the chances slightly favor the Clark Fork. No Clark Fork *tæniodonts* are available for comparison. The species is certainly distinct from any but ?*Psittacotherium lobdelli*, and is very probably distinct from the latter but cannot be rigidly proven to be so on this material."

Dr. Loris S. Russell of the Canadian Geological Survey was kind enough to examine the gastropods. He reports as follows:¹ "These fossils consist of the internal rock of

¹ Letter to the writer May 16, 1933.

land snails. In spite of the imperfect preservation, they can be tentatively identified as *Oreohelix nacimientensis* (White). This was described as *Helix nacimientensis* (Bull. U. S. Geol. Surv. No. 34, p. 26) from the "Puerco" of New Mexico. Field parties under Dr. Walter Granger found the shell in the upper or Torrejon beds, and Cockerell, who studied Granger's specimens, placed the species in *Oreohelix* (Bull. Amer. Mus. Nat. Hist., Vol. 33, p. 103, 1914). This identification suggests that the lower beds of the Ruby formation are of Paleocene age, possibly as old as Torrejon. In the Bighorn basin of Wyoming closely related species of *Oreohelix* occur in the Gray Bull beds (Lower Eocene) but a few scattered shells of the same sort have also been found here in the Upper Paleocene Clark Fork beds."



TEXT-FIG. 13. Diagrammatic section of the Ruby series ('Wasatch' plus Paleocene) in Plateau valley, Mesa Co., Colorado. The crosses mark the fossil-bearing level. The vertical scale is greatly exaggerated.

All the paleontological evidence thus far available indicates a Paleocene age for the *Titanoides* horizon. If, as Simp-

son tentatively suggests, the age is Clark Fork then *T. faberi* is a contemporary of *Coryphodon*. The geological evidence is also suggestive of Paleocene age. *T. faberi* is found some seventy-five feet above the Mesaverde Cretaceous. The beds containing the fossil bearing level consist mainly of a series, some 450 feet in thickness, of finely banded and brightly colored clays with thin sandstone layers intercalated. Immediately above these beds lies an equal thickness of massive sandstone layers with thin clay seams interstratified (fig. 13). The appearance of the whole is almost identical with the early Tertiary stratigraphy of the San Juan basin, as described and illustrated by Sinclair and Granger (1914), in which the basal sandstones of the Wasatch form a capping to the Paleocene sediments. It seems probable that the *Titanoides* level is Upper Paleocene as originally suspected but more precise correlation cannot be given at present. It is to be hoped that knowledge of the contemporary fauna will be increased by the work of the coming season.

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EXPLANATION OF PLATES

- Pl. I. *Titanoides faberi*. Holotype, F.M.N.H. No. P 14637. Skull-ventral view. $\times \frac{1}{2}$.
- Pl. II. *Titanoides faberi*. Holotype, F.M.N.H. No. P 14637. Skull-dorsal view. $\times \frac{1}{2}$.

PLATE I



Titanoides faberi. Holotype, F.M.N.H. No. P 14637. Skull—ventral view. $\times \frac{1}{2}$.



PLATE II



Titanoides faberi. Holotype, F.M.N.H. No. P 14637. Skull—dorsal view. $\times \frac{1}{2}$.

PRELIMINARY EXAMINATION OF ACCUSED PERSONS IN ENGLAND

EDWIN R. KEEDY

(Read April 21, 1933)

A STATUTE enacted in 1327¹ provided: "For the better keeping and maintenance of the Peace, the King will, that in every County good Men and lawful, which be no Maintainers of Evil, or Barretors² in the Country, shall be assigned to keep the Peace." Although knights had been appointed to assist in keeping the peace for over a century,³ this statute may be said to have formally established the office of "keeper of the peace."

In 1344 judicial powers were conferred on keepers of the peace by the provisions of a statute reading as follows: "That two or three of the best of reputation in the counties shall be assigned keepers of the peace by the King's commission, and at what time need shall be, the same, with other wise and learned in the law, shall be assigned by the King's commission to hear and determine felonies and trespasses done against the peace in the same counties, and to inflict punishment reasonably according to law and reason, and the manner of the deed."⁴ Recent investigations disclose that on several occasions previous to the enactment of this statute commissions were granted to keepers of the peace to try felonies and

¹ 1 Edw. III, stat. 2, c. 16.

² This translation is from the Statutes at Large, printed in 1762. The original printed text is: "*queux ne sont mye meyntenours de maloris barretz*," a literal translation of which would seem to be "who are not maintainers of evil barretors." See Statutes of the Realm, I, 257, n. 1. If "ne" be substituted for "de," the translation would convey a clearer meaning, viz. "neither maintainers nor evil barretors." Professor Maitland, in discussing the printing of the Year Books of this period, mentions a case where through the carelessness of the printer "ne" appearing in the manuscript was changed to "de." Publications of Selden Society, XVII, Introd. xxvi.

³ Stubbs, Constitutional History of England (6th ed.), I, 546; Beard, Justice of the Peace, 17; Holdsworth, History of English Law (3d ed.), I, 286.

⁴ 18 Edw. III, stat. 2, c. 2.

trespasses.¹ The judicial powers of the keepers of the peace were enlarged by a statute in 1360, which authorized them "to hear and determine at the King's suit all manner of felonies and trespasses done in the same county, according to the laws and customs aforesaid."² Two years later a statute provided that "in the commissions of justices of the peace" it be mentioned that "the same justices make their sessions four times by the year."³ This statute established the "quarter sessions" and was a formal recognition of the transformation of the "keepers of the peace" into "justices of the peace," as they have since been known.

A series of statutes between 1429 and 1503 gave the justices, in the case of certain specified offenses, the authority to examine the accused when on trial at the quarter sessions.⁴ A learned writer in the 16th century explains this grant of power to the justices as follows: "The obstinacie of evil dooers, that woulde shewe no conscience in acknowledging of their faultes, and the corruption of Jurors that woulde presente nothing that lay onlie in their owne knowledges, hath begotten and broughte into our Lawe, thys tryall by Examination, wherewith it was not before acquainted."⁵ The same writer speaks of forced confessions, "which ye Justices do

¹ Putnam, "Transformation of the Keepers of the Peace into Justices of the Peace," *Royal Historical Society Transactions (Fourth Series)*, XII, 27, 28 and 34.

² 34 Edw. III, c. 1 (7).

³ 36 Edw. III, c. 12.

⁴ 8 Hen. VI, c. 4 (1429); 8 Hen. VI, c. 9 (1429); 8 Edw. IV, c. 2 (1468); 1 Hen. VII, c. 7 (1485); 19 Hen. VII, c. 11 (1503).

⁵ Lambard, *Eirenarcha* (ed. 1582), Bk. II, c. 11, p. 431. In the edition of 1588 Lambard states that he has seen the justices' oath of office expressed in the following verse:

"Do equall right to rich and poore,
as Wit and Law extends:
Give none advice in any cause,
that you before depends:
Your Sessions hold, as Statutes bid:
the forfeits that befall,
See entred well, and then estreat
them to the Cheaquer all:
Receive no fee, but that is given
by Queene, good use, or right:
Ne send Precept to partie selfe,
but to indifferent wight."

Ibid., Bk. I, c. 10, p. 60.

wring out of the partie by ye Examination of him, in such cases wherein examination is permitted."¹ Two of the statutes which authorized the justices to examine the accused at the sessions provided that he might be convicted on his examination alone;² one of these awarded to the justices a tenth part of any fine imposed upon conviction for their labor in obtaining a confession from the accused.³

The power to admit to bail persons arrested for crime, which was originally exercised by the sheriffs as the personal representatives of the Crown, was to a large extent transferred to the justices of the peace by a series of statutes in the fourteenth and fifteenth centuries.⁴ Near the close of the latter century two statutes reflected strikingly divergent attitudes on the part of Parliament towards the practices of the justices in granting bail. In a statute of 1483 it was stated that "forasmuch as divers persons have been daily arrested and imprisoned for suspicion of felony, sometime of malice, and sometime of a light suspicion, and so kept in prison without bail or mainprise, to their great vexation and trouble," it was accordingly provided that every justice of the peace "shall have authority and power, by his or their discretion, to let such prisoners and persons so arrested, to bail or mainprise."⁵ Four years later a statute, after reciting that under the statute of 1483 "divers persons, such as were not mainpernable, were oftentimes letten to bail and mainprise, by justices of the peace, against the due form of the law, whereby many murderers and felons escaped, to the great displeasure of the King, and annoyance of his liege people," provided that the power to grant bail could be exercised only by two justices acting together.⁶

In 1554 a statute was enacted providing that no one shall

¹ *Ibid.* (ed. 1582), Bk. II, c. 9, p. 427.

² 8 Edw. IV, c. 2; 19 Hen. VII, c. 11.

³ 19 Hen. VII, c. 11.

⁴ 4 Edw. III, c. 2 (1350); 34 Edw. III, c. 1 (1360); 1 Rich. III, c. 3 (1483). See Stephen, *History of the Criminal Law of England*, I, 236; Holdsworth, *op. cit.*, IV, 527, n. 4.

⁵ 1 Rich. III, c. 3.

⁶ 3 Hen. VII, c. 3.

be let to bail, other than in open sessions, "except it be by two justices of peace at the least," and providing further that before granting bail the justices "shall take the examination of the said prisoner, and information of them that bring him, of the fact and circumstances thereof, and the same, or as much thereof as shall be material to prove the felony, shall put in writing before they make the same bailment; which said examination, together with the said bailment, the said justices shall certify at the next general gaol-delivery to be holden within the limits of their commission."¹ In 1555 a statute extended the duty of examination to cases where bail was not granted but the prisoner was committed to jail.²

There is a difference of opinion among legal historians as to the purpose and effect of the statute of 1554. Holdsworth, referring to the statutes of 1554 and 1555, says: "These statutes were evidently designed to arm the justices with new powers against prisoners,"³ and also, "They gave, as they were designed to give, the executive some of the advantages against prisoners which were conferred by the inquisitorial procedure of foreign states."⁴ Stephen, however, says that the "system established" by the statute of 1554 "was originally intended to guard against collusion between the justices and the prisoners brought before them."⁵ Stephen's view is supported by the preamble of the statute, which reads that, since the making of the statute of 1487, "one justice of peace in the name of himself and one other of the justices his companion, not making the said justice party nor privy unto the case wherefore the prisoner should be bailed, hath oftentimes by sinister labour and means, set at large the greatest and notablest offenders, such as be not replevisable by the laws of this realm; . . . whereby the said offenders have escaped unpunished, and do daily, to the high displeasure of Almighty God, the great peril of the King and Queen's true subjects,

¹ 1 & 2 Phil. & Mary, c. 13.

² 2 & 3 Phil. & Mary, c. 10.

³ *Op. cit.*, I, 296.

⁴ *Ibid.*, IV, 529.

⁵ *Op. cit.*, I, 237.

and encouragement of all thieves and evil-doers: for reformation whereof," etc. It is also significant that Staunford writing in 1560 refers to this statute as repealing the statute of 1483, but makes no reference to any examination of the prisoner.¹

It would seem that the purpose of the statute of 1555 was different from that of the statute of 1554. This is indicated by the fact that the statute of 1555 provides for examination in cases where no bail is granted and further by the statement in the preamble that the examination of a prisoner who is committed to jail "is as necessary, or rather more than where such prisoner shall be let to bail. . . ." Lambard, in the edition of his *Eirenarcha* which was published in 1588, referring to the statute of 1555, says: "Here you may see (if I bee not deceived) when the examination of a Felon began first to bee warranted amongst us. For at the common law, *Nemo tenebatur prodere seipsum*, and then his fault was not to be wrung out of himselfe, but rather to be discovered by other meanes and men."² It thus appears that while the report

¹ *Les Pleees del Corone*, 75.

² Bk. II, c. 7, p. 213. Before the enactment of the statute of 1555 the Privy Council had on a number of occasions directed justices of the peace to conduct an examination of suspected persons. Note the following records:

"Whereas at the suit of Sir George Bayneham, knight, my Lordes of the Cownsell hadde sent for ij parsons out of Wilshere to be examined towching a murdre of a servaunt of Sir George Bayneham's, slayne by one Thomas Webbe, the same being dewly examined, wer this day sent backe ageyne to the Shiref of Wiltshire to be examined eftsones by him and two other Justyces dwelling nighe unto him, and thereupon to be dismissed or otherwise as shold be thougth unto them expedient." June 8, 1545. *Acts of the Privy Council, 1542-1547*, p. 185.

"A lettre to the Lorde Laware of thanks for his paynes taken in sending up James Norton, and bowlting owf of the hole circumstance of his and others doinges touching the sale of belles and other thinges; requiring his Lordship to call before hym and summe other Justices of Peace of that countie the parishoners of Steyning, causing suche of them as by theyr examinacions shall appere faultie in the matter to be committed to warde, there to remayne untill they shall put in sufficient bonde for the restitution of all those thinges that they have solde, or the just value thereof, to the Kinges use, and to stand to suche farder ordre for theyr contempt as shalbe awarded against them." February 2, 1552. *Ibid.*, 1552-1554, p. 212.

"A lettre to William Kellewey, Robert White and Thomas Pacye, Justices of Peace in the countie of Southampton, to examyn one Jane Woodcock of certain lewde and heynous woordes by her spoken towching the Quenes Heighnes, and if she confesse to have harde them of any other, thenne to committ her to warde untill the reoporters shall have byn examyned; but if she affirme, as she have doon heretofore, that she knoweth the matter by a vysion, in that case to procure, by the best meanes they canne to understand from whence this her wayne opynion ariseth, and to advertise of thier doinges herein." September 14, 1553. *Ibid.*, 547.

of the examination provided for in the statute of 1554 was for the purpose of assuring the Court that bail was properly granted, the examination ordered by the statute of 1555 was for the purpose of securing a confession or other evidence against the prisoner.

Neither of these statutes prescribed the nature of the examination, but as the justices, under the statutes authorizing an examination of the accused when on trial at the quarter sessions, had adopted the practice of interrogating him, it was natural that they should adopt a similar practice when conducting the examination before bail or commitment.¹ This examination, unlike that at the quarter sessions, was not upon oath² and was generally in secret.³

In their examinations under the statutes of 1554 and 1555 the justices did not hesitate to exert pressure upon the accused to confess. Prolonged questionings and confrontations with other witnesses were employed for the purpose of securing confessions. Furthermore, suspected persons refusing to answer were in some cases committed to jail until they were willing to do so.⁴

An illustration of the methods employed appears in the report of the examination in 1612 of a witness and of the accused himself in the case of Robert Creighton, Baron of Sanchar, who was charged with procuring the assassination of one Turner. The report is as follows: "Gray (the witness) then, being by his Majesty's Command examined, confest the whole Truth of the Fact against the Baron of Sanchar; Who likewise by his Majesty's Direction being confronted with Gray, and particularly examined . . . confest by Writing under his own Hand, that he had incited and procured this Assassination, and being prest thereupon by the Questions he discovered a long and inveterate Malice which he had had with all the Occasions and material Circumstances of this Murder."⁵

¹ Bentham states that the examination prescribed by the statute of 1555 was "imported from the continent of Europe." *Rationale of Judicial Evidence*, V, 289.

² Dalton, *The Countrey Justice* (ed. 1619), 273.

³ Stephen, *op. cit.*, 225.

⁴ *The Justice of Peace's Vade Mecum*, 82 (1719).

⁵ 9 Co. Rep. 116, 121a.

Another illustration is found in the case of Colonel James Turner, who was tried for burglary committed against one Tryon. At the trial Sir Thomas Aleyn, a justice of the peace, testified that after being informed of the burglary he interrogated the servants of Colonel Turner. He then stated: "When I had examined these two I went to the examination of Turner, Where he was all that day, where at night? He told me, at several places and taverns and in bed at nine of the clock, and was called out of his bed: but having myself some suspicion of him, I wished him to withdraw. I told Mr. Tryon that I believed if he was not the thief, he knew where the things were. The old gentleman said he could not mistrust him, he had put a great confidence in him; but I desired him to give me leave to charge him with it; and thereupon I called him in, but he denied it, but not as a person of his spirit, which gave me cause for further suspicion." He further testified: "I took Mr. Turner on one side and told him, I did as verily believe if he was not the thief, he could find him out, as I believed I should go home to my wife and children; and I said, that if an angel from Heaven should come and tell me otherwise I could hardly believe it."¹

While the justices had no authority to use torture in their examinations, the records of the Privy Council show that they were sometimes directed to do so by warrant of the Council in the exercise of the Royal Prerogative.² A number of such instances are cited by Jardine in his famous book on *The Use of Torture in the Criminal Law of England*.³ The following are not mentioned by him:

¹ 6 How. St. Tr., 565, 572 (1664).

² "It is clear that the use of torture, though illegal by the common law, was regarded as legal if inflicted under the authority of that extraordinary power of the crown to supersede the common law on occasions of emergency, which was admitted to exist by most people in the time of the Tudors, and by very many in the earlier Stuart period." Holdsworth, *op. cit.*, V, 186.

³ Appendix.

No. 5.

"A Letter to Sir Henry Bedingfelde, Sergeaunt Dier, and Mr. Sollicytor to examin substantially on Nicholas Curat, vehemently suspected of robbing Mr. Keleaway, according to such interrogatories as the said Mr. Keleaway shall deliver unto them for that purpose; and if they shall see cause whie, then to bring him to the racke and to put him to sum pain if he will not confesse otherwise.

"A lettre to the Lorde St. John to cause suche as he hathe alredy apprehended for the ryotte and disorder of late committed upon the

"A like letter to bring one Hughe of Warwicke, suspected for horseteling, to the rack, and to do *ut supra*." December 11, 1555. *Ibid.*, 74.

No. 8.

"A Letter to Sir Roger Cholmeley and Dr. Marten, to repaire to the convict prison at Westminster, and there to procede to the further examination of Sillvester Taverner, prisoner there; who, having embeseled certeine plate and other goods, belonging as well to the Quene's Majestie as to sundry other persons besydes, will by no meanes hitherto declare where the same is become, notwithstanding the matter is allreadie confessed against him by two others. And therefore they are required, for the better atteyning of the truth, to put him to such tortures as by their discretions shall be thought convenient." July 29, 1556. *Ibid.*, 75.

No. 13.

"A Letter to Justice Southcote, to cause one Thomas Andrewes, presently prysoner in the Marshalsey, to be brought to the Towre, and offered the torture of the racke theare, and examine him of his knowledge touchinge a very heinous murder lately comyttyd in Somersetshire, whereof the said Andrewes is vehemently suspected and will hitherto confesse nothing, although he hath been divers tymes examined thereupon. And after he shall have taken his confession, the said Mr. Southcote is willed to return him to the Marshalsey againe to be further proceeded with according to the order of the law.

"A Letter to the Lieutenant of the Tower to cause the said Andrewes, when he shal be brought unto him, to be set to the racke and offered the torture, and to be examined by suche as shall be appointed thereunto by Justice Weston." June 20, 1570 *Ibid.*, 77.

No. 19.

"A Letter to Thomas Townsend, Henry Doyly, and William Blennerhasset. That wher Their Lordships understande that the house of Sir Drew Drury, Knight, called Catton, hath of late bene robbed by certain rude persons, with the privitie of one Humfrey, a boy dwelling in the house; who, being since committed and examined touching the said robbery, refuseth to discover the reste of his complices; they are therefore required to call the said Humfrey before them, and to use the best means they may to induce him to confesse the robbery; which if he shall obstinately refuse to doe, then are they required by some slight kinde of torture, such as may not touch the losse of any lymbe, as by whipping, wring from him the knowledge of the persons and manner of the robbery; that thereupon order may be taken for their apprehension and punishment according to the lawes, &c." December 9, 1580. *Ibid.*, 82.

No. 33.

"A Letter to Sir Owen Hopton, Mr. Daniell, Mr. Yonge; that whereas of late there were discovered certaine lud persons, who were to be charged with disobedience, misbehaviour, and practices against the state and present government, which allreadie were examined by Richard Yonge, Esquier, but would not be brought by faire meanes and good persuasions to utter their knowledge in divers matters concerning Her Majestie and the State; They are required to call to them the said Mr. Yonge, and to examine such persons as were sent inclosed contained in a schedule, especiallie John Staughton and Humfrey Fullwood, who were deplier charged than the rest; and if they should shew themselves obstinate and perverse as they have done heretofore, that they should carrie them to the Tower, there to be kept close prisoners, and to be putt to the racke and torture to compell them to utter their uttermost knowledge in all matters they dealt in or are privie unto." January 7, 1587. *Ibid.*, 92.

goodes and corne of Jane Stourton to be diligently examined who were present besides themselves at the act doing, and if they shall not be plaine therein, than to put them to sum torture for the better trieng out of the truthe, and upon understanding who were the rest he is willed to give order for their apprehencion accordingly, and to committe them all to sure and straight prison in irons, without baile of (*sic*) mainprise, untill Mighelmas Terme next, and in meane tyme to procede to their enditement, and to signify the same with the examinacions he shall take of them into the Starre Chamber at the beginneng of the next Terme . . .".¹

"A letter to Mr. Justice Southcotte, Sir Owen Hopton and Sir Thomas Browne, knightes, and Robert Levesey, esquire, that where by a letter from Mr. Browne and other Justices of Surrey their Lordships do understande what hathe ben don in the examining of Robert Wintershall, Harvey Mellershe, and others suspected for the murther committed in December last uppon the persons of Richard Mellershe of Dounford in that countie and Thomas his sonne, and where it appeareth by the said letter that upon their examinacions nothing of moment can be discovered that maie inforce their condemnation; for whiche cause (the contry also expecting an ende thereof) their Lordships do require them withe some convenient speede to proceed to a new examination of the said Wintershall, Mellershe and the reste, severing them as well into places where they maie remaine asunder, as severallie to examyn them, using the best meanes they can to induce them to confesse the troathe (*sic*). Whereunto (yf by no meanes they shalbe broughte) then are they required to deale withe them by shewe of some terror to be offered unto them by committing them to the dungeons and like places of obscuritie in the Tower, appointing unto them a shorte proportion of diet accordingly. And to that ende their Lordships do require him, Mr. Lieutenante, to receive them into his custodie, and to se them bestowed in places, and severed in places within the Tower, as is aforesaid, and there (yf it shalbe nedefull) to be further terrified by shewing unto them the Racke or otherwise, as they shall thincke meete, where (joyning together) they are required to continewe their paynes in examining of them from tyme to tyme to bring them to confesse the facte, that thereupon (sufficient matter appearing) they maie be further proceeded withall, according to lawe."²

"A letter to Mr. Justice Younge. Wee have understoode the paines you have taken in th' examininge of the fower persons lately committed by you unto Newgate upon suspicion of a robbery lately

¹ July 24, 1557. Acts of the Privy Council, 1556-1558, p. 130.

² June 6, 1579. *Ibid.*, 1578-1580, p. 157.

donne at Wickham in Kent, and the discrete meanes you have used to discover the authors of that lewde facte, wherin wee do greatly allowe of the good endeavor you have used to bringe forth the truth of so fowle an acte. But because the proofes are so manifest and evident against them, thoughe they will not be brought to confesse the same, wee have thought yt meete that you shall by virtue hereof remove them to Brydewell, whom upon sight hereof the officers ther shall receave, and ther you shall with the assistaunce of some of the Justices see them to be rexamined, and if they will not be brought to confesse the whole truth of that robbery and who were the rest of their complices, then you shall cause them to be put to the racke and torture of the manacles, that they may be compelled to utter all their followers, partakers and abbettors of that robbery, and that which is fitt to be knowne touchinge the perfecte discovery of so lewde a facte. In the meane tyme wee are to warne you that none of them by any meanes may be bailed. *Postscript*:—Amonget others which you are precisely to examine wee require you especially to bolte forth the truth in ministringe the torture to William Browne, a butcher, who knoweth the whole society of theis wicked disposed persons."¹

The interrogation of the prisoner played such an important part in the administration of justice in the sixteenth and seventeenth centuries that detailed instructions were prepared setting forth what circumstances were to be considered by the justices in examining the prisoner. Some of these are in striking contrast to modern principles of proof. Following is the list of such "circumstances," as prescribed by Dalton:²

- "1. His name; scz. if he be not called by divers names.
2. His parents, if they were wicked, and given to the same kind of fault.
3. His ability of body; scz. if strong and swift, or weake or sickly not likely to do the act.
4. His nature, if civill or hasty, witty and subtyll, a quarreller, pilferer, or bloody minded &c.
5. His meanes; if he hath whereon to live, or not.
6. His trade; for if a man liveth idly or vagrant (*nullam exercens artem nec laborem*) it is a good cause to arrest him upon suspicion, if there have been any felony committed.

¹ Apr. 18, 1590. *Ibid.*, 1590, p. 69.

² *Op. cit.*, 275. See also Crompton, *Loffice et auctoritie de Justices de peace* (ed. 1583), 64b; Lambard, *op. cit.*, (ed. 1588), Bk. II, c. 7, p. 220.

7. His company; if ruffians, suspected persons, or his being in company with any the offenders.
8. His course of life; scz. if a common alehouse-hanter, or ryottous in dyet, play, or apparrell.
9. Whether he be of evill fame, or report.
10. Whether he hath committed the like offence before, or if he hath had a pardon, or been acquitted for felonie before;
Nam qui semel est malus, semper presumitur esse malus, in eodem genere mali.
11. If he hath any blood about him.
12. If any of the goods stollen, be in his possession.
13. The change of his countenance, his blushing, looking downwards, silence, trembling.
14. His answers doubtful, or repugnant.
15. If he offered agreement or composition.
16. The measure of his foot, or horse foot.
17. The bleeding of the dead body in his presence.
18. If, being charged with the felony, or called theefe, he saith nothing.
19. If he fled; *fatetur facinus, qui Judicium fugit.*
20. Place; scz. if convenient for such act, as in a house, in a Wood, Dale, &c.
21. Time; the yeare, day, houre, early or late.
22. Where the offender was at the time of the fact, and where the day or night before; his businesse, and company there, and wnesse to prove all these.
23. Manner; if willingly, by chance, or necessitie.
24. If former malice.
25. If to his benefite, or what hope of gaine.
26. If for the eschuing of any hurt, or danger."

The report of the interrogation was given great weight at the trial and although the rule was that a confession made in response to the questioning of the justices was not alone sufficient evidence to justify conviction,¹ Dalton mentions a case where conviction and sentence of death were based solely on such a confession.²

In the early part of the nineteenth century, the interrogation of the accused following his arrest ceased to be the accepted practice. While records of such examination have

¹ Dalton, *op. cit.*, 277

² *Ibid.* (ed. 1666), 352.

been found as late as 1826,¹ there were cases where the court ruled that such interrogation was improper and that confessions thereby obtained were not admissible in evidence against the accused at the trial.² The changed attitude is evidenced by the following extract from a book relating to the office and duties of a justice of the peace published in 1822: "The excessive mildness usual in the exercise of English jurisprudence, renders it the duty of the magistrate to apprise the prisoner that his examination may be produced on his trial, and to give him a reasonable caution, that he is not required to criminate himself."³

In 1826 a statute was passed which *inter alia* reenacted the provisions of the statutes of 1554 and 1555, prescribing the "examination" of the prisoner by the magistrates before bailing or committing him.⁴ It was very doubtful, however, whether it was the intention of Parliament, in again providing for an "examination," to reestablish the practice of interrogating the accused as was customary under the statutes of 1554 and 1555. Sir Robert Peel, the Home Secretary, when he presented the bill in the House of Commons, referring to methods of trial, stated the following: "There are provisions in the criminal law of France, calculated no doubt in individual instances, to elicit truth, but which I should never wish to see ingrafted on the practice of this country. I should deprecate anything approaching to the compulsory examination of an accused party."⁵ The debates upon the bill do not indicate that the members of Parliament thought the bill authorized the interrogation of the prisoner.

¹ *Rex v. Ellis*, Ry. & M. 432. See also *Rex v. Carlisle* (1824), cited in Starkie, *Law of Evidence*, III, Appendix to Part IV, 52.

² *Rex v. Wilson*, 1 Holt, N. P. Rep. 597 (1817); *Rex v. Fagg*, 4 C. & P. 566 (1831). See also *Rex v. Gilham*, 1 Moody C. C. 186, 191 (1828); *Rex v. Green*, 5 C. & P. 312 (1832); *Reg. v. Arnold*, 8 C. & P. 621 (1838).

³ Dickinson, *Justice of the Peace*, 626.

⁴ "That the Two Justices of the Peace, before they shall admit to Bail, and the Justice or Justices, before he or they shall commit to Prison, any person arrested for Felony or on Suspicion of Felony, shall take the Examination of such Person and the Information upon Oath of those who shall know the Facts and Circumstances of the Case, and shall put the same, or as much thereof as shall be material, into Writing; and the Two Justices shall certify such Bailment in Writing." 7 Geo. IV, c. 64, s. 2.

⁵ 14 Hansard, *Parliamentary Debates*, N. S., 1233.

In 1848 a statute was enacted which gave the prisoner the privilege of making a "statement" after being advised that he need not say anything unless he desired and that whatever he said might be used in evidence against him.¹ The language of this statute would seem to create a procedure markedly different from that provided by the statute of 1826, which, as stated, reenacted the provisions of the statutes of 1554 and 1555 authorizing "examination of the prisoner."² An investigation, however, discloses the fact that the bill was not debated at any stage either by the Lords or the Commons, — a most unusual proceeding if a bill provides for a substantial change in criminal practice. More significant, however, is the statement of Sir John Jervis, the Attorney General, in asking for leave to present this bill and another one relating to the functions of examining justices. He said: "In these two Bills he had endeavored to introduce nothing new; . . . his object had been simply to collect together the enactments and decisions forming the existing law upon these heads."³ This statement clearly shows that the Attorney General regarded the act as simply a codification of the existing practice. It is also to be noted that the bill was enacted as presented.

The decline in the practice of questioning the accused at the preliminary examination, which occurred before the enactment of the statute of 1848, was due to a number of contributing causes. It may be safely said that the principal one was a general reaction against the oppressive methods of the preceding centuries. This reaction had already been manifested

¹ 11 & 12 Vict. c. 42, s. 18.

² "The statutes of Philip and Mary already referred to, repealed and reenacted in 1826 by 7 Geo. 4, c. 64, authorized committing magistrates to 'take the examination' of the person suspected. This examination (unless it was taken upon oath, which was regarded as moral compulsion), might be given in evidence against the prisoner. This state of the law continued till the year 1848, when by the 11 and 12 Vic. c. 42, the present system was established, under which the prisoner is asked whether he wishes to say anything, and is warned that if he chooses to do so what he says will be taken down and may be given in evidence on his trial." Stephen, *op. cit.*, 441.

"But when we pass from the second to the third quarter of the nineteenth century, we find that the Parliament of Queen Victoria has taken a widely different course from the Parliament of King Philip and Queen Mary." Pollock, *Expansion of the Common Law*, 31. See also Holdsworth, *op. cit.*, I, 296, 297.

³ 96 Hansard, Parliamentary Debates, 3D. S., 5.

in the dying out of the habit of interrogating the accused at the trial, which occurred about the beginning of the eighteenth century;¹ the establishment near the end of this century of the rule that confessions obtained by threats or promises were inadmissible in evidence;² and the growing practice of permitting the accused to be represented by counsel at the preliminary examination.³ Further reasons for the change are found in the creation of the office of stipendiary magistrate⁴ and in the establishment of a professional police force which took over the work of detecting and investigating crime.⁵

As a result of the Act of 1848, the right of the accused to be represented by counsel was recognized, and he was accorded the privilege of having the witnesses examined in his presence.⁶ Although the Act prescribes that the place where the examination is conducted "shall not be deemed an open court,"⁷ in practice the proceedings are open to the public.⁸

It will thus be seen that through a process of evolution the preliminary examination developed from an inquisitorial into a judicial proceeding.

¹ See Stephen, *op. cit.*, 440; Wigmore, *Evidence* (2d ed.), s. 2250 (3).

² *Rex v. Warickshall*, 1 Leach C. C. 298 (1783). See also Wigmore, *op. cit.*, s. 819.

³ "It is true, that in practice, magistrates do permit, on many occasions, the presence of advocates for the parties accused." Abbott, C. J., in *Cox v. Coleridge*, 1 B. & C. 37, 49 (1822).

⁴ 32 Geo. III, c. 53 (1792). The statute provided for a yearly salary of £400. This amount was increased by later acts. Referring to these acts, Maitland states the following: "What this indicates is the great change which during this period is making the duties of the justice in criminal cases more and more judicial." *Justice and Police*, 100. In 1839 it was provided by statute that stipendiary magistrates must be barristers of at least seven years' standing. 2 and 3 Vict., c. 71, s. 3.

⁵ 10 Geo. IV, c. 44. See Maitland, *op. cit.*, 109; Pike, *History of Crime in England*, II, 459.

⁶ See *Reg. v. Griffiths*, 54 L. T. 280 (1886) and Alexander, *The Administration of Criminal Justice*, 26.

⁷ S. 19.

⁸ "The secret inquisitorial proceeding has become open and judicial." Pollock, *op. cit.*, 31. See also Alexander, *op. cit.*, 26.

To General Lafayette

Sir

While all the Clases of our Citizens are vying with each other to welcome the adopted Son of Washington, and of our Country, The members of the American Philosophical Society seize with joy this happy opportunity to testify their respect for the generous Warrior, who first came to the aid of the cause of American freedom, and after so long a separation, to take their loved associate once more affectionately by the hand.

In you, Sir, we not only revere the Hero & the patriot, but we also cherish the lover of Science, and the friend of our immortal Franklin. You have enjoyed the intimacy of that great man; you have often heard wisdom flow from his lips, and he was fortunate enough, after co-operating with Washington and Yourself in the glorious work of American Independence, to live to witness your noble efforts in the cause of liberty in France. Still happier is the fate of our Patriot Jefferson. He yet lives to press you to his bosom, and communicate with you the various successes of this eventful age, in which you have both acted a principal part. We hope you will soon see him in his philosophical retirement; you will bear to him the expression of our grateful remembrance, and he will tell you, that the members of this Society, have never ceased to be impressed with feelings of the tenderest affection for their illustrious Brother, General Lafayette.

In behalf of the American
Philosophical Society
(The Office of President being vacant)
Peter S. De Pauw,
Vice President

LAFAYETTE AND THE AMERICAN PHILOSOPHICAL SOCIETY

J. BENNETT NOLAN

THE American Philosophical Society has recently acquired a Lafayette souvenir of unique appeal, the original testimonial given to the General a century ago by his admiring fellow-members of the Society, and now appropriately returned for display in the same Assembly Hall where it was first presented Friday, October 1st, 1824. The document was discovered last summer in France amongst a bundle of letters written to Lafayette during his memorable American tour of 1824-25. The General had carefully numbered these missives and put them away in the garret of his chateau at Chavaignac. From that time it is not probable that six people have seen this testimonial until its recent re-appearance in Philadelphia.

The dexterous Capuchins, Macaulay tells us in his essay on Milton, never chose to lecture on the merits of a saint until they had inflamed the devotional spirit of their auditors by the exposition of some appropriate relic, a lock of the hair perhaps or a portion of the holy garment. The resurrection of this relic may serve as an excuse to recall the long and close connection of the Marquis with the American Philosophical Society. It is the more timely, in that preparations are now in full swing, under the auspices of the recently formed society of the American Friends of Lafayette, to commemorate, next year, the one hundredth anniversary of his death. Lafayette died in his stately mansion on the Rue de Anjou in Paris, May 20th, 1834.

January 19th, 1781, nine months before my Lord Cornwallis marched out from Yorktown to the tune of "The World Turned Upside Down," a meeting of the American Philosophical Society was held for the election of candidates. The members assembled at Carpenters Hall where the

Society's effects had reposed since their removal from the rooms of the University of Pennsylvania, June 16th, 1780. Benjamin Franklin had unanimously been elected President two weeks before but he was serving as our envoy at Paris and it is probable that in his absence David Rittenhouse presided as Vice President. Twenty-one members of the Society attended and the brief and faulty minute as published in the volume of the Proceedings published by the Historical Society in 1884 is as follows:

"1781. Jan. 19.—(21 present.)

LaFayette, Ebenezer Hazard, Jared Ingersoll and four other new members elected."

A reference to the original minutes shows the inadequacy of the printed record:

"Friday, January 19 1781.

Present, Dr. Bond, D. Rittenhouse, Jas. Wilson, Thos. McKean, George Bryan, Wm. White, John Ewing, Mr. Kunze, Geo. Duffield, Dr. Duffield, J. B. Smith, O. Biddle, C. Biddle, DuSimitiere, T. Bondjunt, Dr. Hutchinson, F. Hopkinson, T. Matlack, Lewis Nicola, M.^d D. Marbois & James Davidson.

On motion, The list of Gentlemen in nomination, agreeably to the rules of the Society, for new members, was read the Society then proceeded to ballot for them, in the order in which they had been nominated, and the following Gentlemen were elected, viz.

1. Le Marquis de la Fayette, Major General in the army of the United States of America.
2. Ebenezer Hazard, Esq.
3. The honorable Thomas Bee Esq. of South Carolina
4. Dr. Hugh Shiel, of Philadelphia
5. Isaac Gray of Philadelphia
6. Le Chevalieur de Chatellux, Marshall of the Field in the Army of France, Chevalier of the Royal Military order of St. Louis and one of the forty members of the French Academy

and 7. Jared Ingersoll Esq. of Philadelphia.

Mr. Du Marbois presented to the Society, a pamphlet in French, containing an account of, and proposals for printing a work of great

merit entitled "*Voyages Metallurgiques, ou Recherches et Observations sur les mines; par feu M. Jars, de l'Academie Royale des Sciences, 3 vol. in 4° enrichis d'un grand nombre de Planches en taille done, très-bein gravées*".

Lafayette had been in Philadelphia during the closing weeks of the previous year, 1780. Chastellux who was elected to the Philosophical Society at the same sitting records that he met Lafayette at Washington's camp near Pompton, New Jersey some weeks before and had been introduced by him to the Commander-in-Chief. Apparently the Marquis did not accompany Chastellux upon his journey to Philadelphia for the latter speaks only of the escort of Colonel Moylan and an aide-de-camp. When Lafayette came to the city, however, the two Frenchmen were inseparable. Together they visited the battlefields of Germantown and of Brandywine, attended a meeting of the Dancing Assembly and dined with James Wilson, at whose festive board the jovial Richard Peters sang a song of his own composition "So Jolly and so free that I shall dispense with giving either a translation or an extract." as Chastellux records. Both of the illustrious visitors were proposed on the same night for membership in the Philadelphia Academy, upon which occasion, to the embarrassment of the members present, Lafayette was at first blackballed although later elected. Neither Lafayette nor Chastellux was in Philadelphia on the day of their election to the Philosophical Society, January 19th, 1781. Chastellux had departed upon his tour of the Middle States and Lafayette had gone back to camp.

Lafayette took part in the Virginia campaign and was present at its triumphal close before Yorktown. In December 1781 he returned to France and remained there while the war drew to a tedious close. That he did not forget the renowned Society in Philadelphia which had honored him with membership is shown by the Society's printed minute of April 2nd, 1784:

"LaFayette's letter enclosing an authentic narrative of experiments lately made in France with air balloons."

Here again it is preferable to turn from the condensed printed record to the more illuminative original minute:

"A Letter from the Marquis la Fayette dated Paris Dec. 10th 1784 inclosing an authentic Narrative of the Experiments lately made in France with air Balloons, drawn up by Mr. Sage, an able Cheymist in the Academy of Sciences, with two Copper Plates Prints of those machines, was presented to the Society and read."

At the next meeting, April 16th, 1784, the record was made:

"LaFayette's packet duplicated by one of the secretaries."

The Marquis returned to the country which owed its independence so largely to his enthusiasm in the following summer. On August 4th, 1784, he landed at New York from the ship *Courrier de New York*, to visit the city which he had only regarded previously from a distance while it was being held by the enemy. He came almost immediately to Philadelphia where was arranged a special meeting in his honor. At this assemblage, at which twenty-two of the members were present:

"LaFayette 'entertained them with a particular relation of the wonderful effects of a certain invisible power, in nature, called *animal magnetism* lately discovered by Mr. Mesmer, a German Philosopher, and explained by him to a number of Gentlemen in Paris of which number the Marquis was himself one. By this Relation it appears that persons may be so impregnated with this power (by a process which the Marquis does not think himself at liberty yet to explain) as to exhibit many phenomena similar to those of metallic magnetism'."

The French Revolution ensued and in the crowded eventful years which followed Lafayette had little opportunity for writing to his scientific friends in Philadelphia. He went into prison at Olmutz, and then to his German asylum. His son, George Washington Lafayette, arrived after a sojourn of six years in America and may have brought some news from Philadelphia. In any event, after his return to France, the General's thoughts reverted once more to the Philosophical

Society, and in October, 1805, he sent their library the two volumes of Destutt Tracy's *Project d'Elements de Ideologie* which belated recognition was duly acknowledged by the Secretary.

Napoleon became emperor, departed for his Elban exile, came back for the Hundred Days, and was succeeded by the dull Bourbon king without apparent correspondence between Lafayette and the Philosophical Society of Philadelphia.

Two decades had elapsed since the receipt of Lafayette's books when the Society took cognizance of the expected arrival of the Marquis as the Nation's Guest. Of the twenty-two members who had met with him in the Carpenters Hall on that forgotten August day in 1784, only Bishop White and the venerable Judge Peters remained. The officers felt that in the nation-wide preparation for the fitting reception of the great Marquis some gesture was expected from them, particularly as the General was still enrolled as an honored member. On motion of Mr. Vaughan it was resolved:

"That a committee be appointed to make arrangements for the proper reception of our illustrious associate General LaFayette; to ascertain when it may be convenient to him to meet the Society; to prepare an address to be delivered on the occasion; and to call a special meeting at the time which the General shall appoint."

The Society at this time was without a president, for the eminent Robert Patterson had died a month before and the chair was temporarily occupied by the vice president, Peter S. DuPonceau, a Frenchman by birth, and prominently identified with the social and public life of Philadelphia in the first three decades of the last century. Mr. DuPonceau began his public life as an abbé of the French Church and died in Philadelphia in 1844 after a life replete with vicissitude. Oddly enough he did not succeed as president, that honor being accorded to Chief Justice William Tilghman, and it was only after Justice Tilghman's death in April, 1827, that Mr. DuPonceau was elevated.

When it became known that Lafayette and his suite had left Havre on the *Cadmus* and were expected in New York

about the middle of August the Philadelphia Reception Committee organized and held frequent meetings. Joseph S. Lewis of the committee was sent to New York to await the arrival of the Nation's Guest and secure a formal appointment for the municipal reception. Mr. Lewis witnessed the General's triumphant debarkation at the Battery on August 15th, and attended the fetes given in his honor, taking critical notes the while for the edification of his committee:

"From what I have seen here we have no fear for Philadelphia in the display we shall make."

he somewhat superciliously wrote to Benjamin Tilghman.

While in New York Lewis received a letter from Mr. DuPonceau at Philadelphia under date of September 25th, 1824, enclosing a draft of the proposed Address of the American Philosophical Society, the same Address now so providentially returned after a century of exile.

"I beg that the members of the committee who will go to visit the General will be so good as to take charge of it (the address) and of the two letters enclosed, one from the Philosophical Society inviting the General to their sitting on Friday, the 1st of October in the evening, the other from French citizens requesting his company at dinner on Monday, October 5th.

"I beg leave to observe to you that among the numerous addresses to be presented to the General, some will have to be delivered by the same person, therefore, that some understanding will perhaps be necessary to avoid confusion."

Mr. DuPonceau's anxiety as to the duplication of orators probably arose from the fact that he himself served in a double capacity, presenting the memorials both of the Philadelphia Bar and of the Philosophical Society.

Meanwhile the members of the Society in Philadelphia had not been idle. On Thursday, September 23rd, Dr. R. M. Patterson wrote to Benjamin Tilghman of the Philadelphia Committee of Arrangements:

"Mr. Vaughan and I have called on behalf of the Committee of the American Philosophical Society to consult with you on the subject of their reception to General LaFayette. It is their wish to

be introduced to the General soon after his arrival and to know when they can be conveniently received. They will invite the General to be present at a meeting of the Society and as there will be a stated meeting on Friday, the 1st of October, they would be glad to have that evening appropriated for them, if this can be made consistent with the other arrangements of your committee. The Society's address is with Mr. DuPonceau."

And now came the definite announcement that the General would set foot on the sacred soil of Pennsylvania on Monday morning, September 27th, he having tarried the Sunday at Trenton "in order to go to church" and to call upon the ex-King of Spain, Joseph Bonaparte, at Bordentown.

The city was in a fever of excited preparation. Governor Shulze had left his home in Lebanon the Wednesday previous, spent the night at the home of Attorney General Frederick Smith in Reading, and arrived in Philadelphia on Friday morning. The militia from Berks, Bucks and Montgomery County had drawn into the metropolis and the City Troop were in martial array. Good Mayor Watson, the same punctilious executive who at the civic ball given in Lafayette's honor, formally stipulated,

"Usual ball dress must be worn. No gentlemen will be admitted in boots."

was closeted in his residence nervously conning over his Address of Welcome.

On Wednesday, September 29th, to the peal of bells, the boom of cannon from the warships in the harbor, and the acclaim of the populace, the Nation's Guest made his historic entry into Philadelphia. The two following days were so replete with receptions, parades, banquets and presentations that one wonders when the General found time for repose.

At last on Friday evening, October 1st, Lafayette left his quarters at the Mansion House on Third Street above Spruce to fulfill his appointment at the Philosophical Society. It had been a busy day, but the General found time to diverge from his direct route to the hall of the Society for one of those gracious gestures which so endeared him to our people. On

South Fourth Street below Pine there dwelt a colored woman named Hannah Till, reputed to have been over one hundred years old. She had been cook for Lafayette in the Revolution, and afterwards in Philadelphia during his visit of 1784. Somehow, the General learned that "Aunt Hannah's" home was encumbered with a mortgage, and he drove around to her house to assure her personally that he would have the mortgage paid off.

After this affable interlude he drove down Chestnut Street under the great arch erected in his honor, passed the door of Independence Hall where, in 1777, he had waited as a forlorn adventurer while an obtuse and discourteous Congress debated within doors as to whether they should accept his services, turned south on Fifth Street to the building which the Society had completed in 1789 and which it still occupies.

In the dignified Assembly Hall a notable company was gathered. Joseph Hopkinson was there and Major General Izard, Bishop William White and Dr. Bache, Roberts Vaux and Charles W. Peale, an audience worthy of the occasion and the guest.

The Marquis took his seat of honor and the vice president read the testimonial, the relic herewith illustrated. It differs from the generality of the fulsome greetings proffered during the tour by its touching reference to one of the few of Lafayette's Revolutionary compatriots who still lived to greet him:

"Still happier is the fate of our Patriarch Jefferson. He yet lives to press you to his bosom, and commemorate with you the various successes of this eventful age, in which you have both acted a principal part. We hope you will soon see him in his philosophical retirement, you will bear to him the expression of our grateful remembrance, and he will tell you, that the members of this Society, have never ceased to be impressed with feelings of the tenderest affection for their illustrious Brother, General LaFayette."

This reference attains an added fitness from the circumstance that Jefferson, then eighty-one years old, had himself been president of the Society. Even at his advanced age he was so fearful that he might not have the opportunity of seeing



THE NATION'S GUEST ARRIVES AT YORK

From a contemporary sketch



Lafayette once more that he actually meditated a trip to Yorktown from Monticello over the impossible Virginia roads, and the editor of the Richmond Compiler observed:

"We are apprehensive that Mr. Jefferson will be unable to visit Richmond or Yorktown. He is anxious to pay every respect to LaFayette but we understand that his state of health would scarcely permit him to go so far from home."

The Patriarch was spared the ordeal of a trying journey when Lafayette graciously announced his intention of paying a visit to Monticello.

After the presentation of the testimonial the routine of the Society was resumed and Mr. C. J. Ingersoll read a paper on "The Improvement of Government" after which it was

"Resolved, That the Librarian be directed to present to General LaFayette a copy of the New Series of our Transactions, a copy of our Historical Transactions, and a copy of our Catalogue, all handsomely bound."

The response of the General is given in the National Gazette of the following day which quotes him as having:

"Declared the high sense he had ever entertained of the honor of being one of the members. He warmly expressed pleasure which he anticipated as an old member of the Society in meeting them that evening."

A reception ensued and then Lafayette went on to the residence of Nicholas Biddle at 273 Chestnut Street "where he remained the balance of the evening."

The General departed upon his triumphant tour of America and sailed from Washington in September of the following year. He never again attended a meeting of the American Philosophical Society, but the recollection of his memorable visit lingered long in the memory of the participants.

In February, 1827, the Society learned of the death of Count Lasteyrie, son-in-law of General Lafayette, and passed an appropriate minute of condolence with directions that it be sent to the General at LaGrange.

On March 6th, 1829, the gift of a bust of Lafayette from

Dr. Chapman was duly recorded, the same graceful memorial which now adorns the Hall of the Society.

The decisive part taken by the Marquis in the July Revolution of 1830 was followed with interest by his fellow members of the Philosophical Society and then with the belated mail of June 20th, 1834, came the news of his death a month before. Mr. DuPonceau was now in the Chair.

"The President, with the expression of deep feeling, announced to the Society the death of their illustrious associate, General LaFayette. On this information being received, the Society resolved to dispense with the Transaction of the ordinary business of the Society."

The association which had begun fifty-four years before in the rooms in Carpenters Hall in the darkest hour of the Revolution was now terminated, and the members of the Philosophical Society in testimony of their bereavement wore crape on their left arms for the space of one month.

The last of the brilliant assemblage which met on that Autumn evening of 1824 to honor Lafayette has long since been gathered to his fathers. Of the busy thousands who daily pass under the historic Hall in Fifth Street, few, it is to be supposed, look up to the windows where the debonair Marquis once stood or pause to reflect upon the historic association which the building embodies. There remains only this yellowed testimonial so recently and fortuitously restored to remind us of a great day long gone when a thankful people united in their enthusiastic plaudits to the Nation's Guest.

THE FISH FAUNA OF BEARTOOTH BUTTE, WYOMING

PARTS II AND III

WILLIAM L. BRYANT

WITH AN APPENDIX: EURYPTERIDS FROM THE LOWER DEVONIAN OF BEARTOOTH BUTTE, WYOMING, BY RUDOLPH RUEDEMANN

PART II. PISCES

Order *Arthrodira*

Family *Acanthaspida*

NUMEROUS remains of Acanthaspid fishes occur in the Beartooth fish-lens. These consist of detached head roofs and trunk plates. While the bones show no evidence of having been mechanically rolled or waterworn, unfortunately, only in a few instances, are they so associated as to indicate that they belonged to the same individual.

Although widely distributed, this family is one of the rarest among Devonian fishes. First known from the United States by detached plates of the latero-ventral armor, remains of Acanthaspids were later found in Eastern Canada and in various localities in northern Europe. In recent years a large number of Acanthaspids have been discovered in the Lower Devonian rocks of Spitzbergen and Germany. The forms from Spitzbergen were described by Anatol Heintz,¹ and those from Germany by Ferdinand Broili² and Walter Gross.³ It is of interest to note that a Psilophyton-like flora occurs in the Lower Devonian beds of Gemünden, in which are found

¹ Anatol Heintz, Die Downtonischen und Devonischen Vertebraten von Spitzbergen. II Acanthaspida; Kong. Dept. Handel, Sjøfart, Industri, Handwerk og Fiskeri; Skrifter om Svalbard og Ishavet Oslo, 1929. Nos. 22, 23.

² Ferdinand Broili, "Acanthaspiden aus dem rheinischen Unterdevon." Sitzb. d. Bayerischen Akad. d. Wissenschaften mathem.-naturw., Abt. 1929, Heft II. Neue Beobachtungen an Lunaspis 1930, Heft I.

³ Walter Gross, "Die unterdevonischen Fische und Gigantotraken von Overath." Abhandl. der Preuss. Geol. Landesanstalt. Neue Folge, 1933. Heft 145.



remains of the Acanthaspid, *Lunaspis*, described by Broili; for a related flora is also found in the fish beds of Beartooth Butte.

Finally, Branson and Mehl¹ lately described a portion of the trunk armor of an undoubted Acanthaspid fish from Devonian rocks near Blacksmith Fork, Utah.

It is now well known that the Acanthaspids are primitive Arthrodires, but the systematic position of the *Arthrodira* as a group is much less certain. Among recent authors, Stensio considers the *Arthrodira* to be true fishes related to the *Antiarcha* and derived from some offshoot of the *Elasmobranchii*, while Heintz in his late memoir on *Dinichthys* proposes to place the *Arthrodira* together with the *Antiarcha* in an independent class equal in rank with cyclostomes and fishes. This conclusion is based partly upon the theory that the head of the Arthrodire was movably connected to the body armor by a pair of neck-joints functioning as a part of the jaw mechanism, that true teeth, dentine or enamel, do not occur in the Arthrodires, and that their jaws cannot be homologous with the jaws of other vertebrates.

In my opinion, we still lack sufficient detailed knowledge of the *Arthrodira*, and of their evolutionary history, to warrant their removal from the class *Pisces*. Whatever the jaw mechanism of the ancestral Arthrodires may have been, it seems certain that it progressively developed from the time when these animals became actively predaceous. The neck-joints in *Dinichthys* are exceedingly ingenious. They are of the ball and socket type and are provided with sturdy flanges that limit the arc in which the head might be moved up and down. One finds upon the underside of the head-roof in *Dinichthys*, and upon certain plates of the body-armor, ridges and depressions which are reasonably supposed to have been the seats of attachment for powerful muscles that raised and lowered the head, perhaps affording a more powerful bite. In the more ancient Coccosteids these keels and depressions on the underside of the head-roof and trunk armor are propor-

¹ E. B. Branson and M. G. Mehl, "Fishes of the Jefferson Formation of Utah," *Journal of Geology*, Vol. XXXIX, 1931.

tionately much less developed, while in the still more primitive Acanthaspids, especially in those from Beartooth Butte, some are entirely absent. Thus there is no keel on the inner side of the median dorsal plate nor on the antero-laterals. The ridges and depressions on the inner side of the head-roof, while resembling those of *Dinichthys* and *Coccosteus*, are much weaker than in either. At the same time, in the Beartooth Acanthaspids hardly any traces are to be found of the highly specialized ball and socket neck-joints developed in the later Arthrodires. Instead, the head-roof overlaps the antero-dorso-lateral plates to a considerable extent. If the head moved independently, as doubtless it did to a limited extent, the functional hinge must have been located in a long, shallow depression running across the fore part of the ADL (Pl. XIV, Fig. 2).

No traces of the jaws or dentition have ever been found in the Acanthaspids. They must have been present, of course, and we must therefore suppose that the gnathal elements in the Arthrodires were, originally at least, partly cartilaginous.

The question as to the presence of true teeth in the *Arthrodira* is of great importance. As Stetson¹ remarks, "If the 'teeth' were true dentine and enamel, the evidence would be fairly strong for jaws of the gnathostome type. If not, though not precluding the possibility of gnathostome origin, the weight of the evidence is all on the side of their being modified dermal plates."

As is well known the jaws in *Coccosteus* and later Arthrodires consist of a pair of elements below (infero-gnathals), which bite against two paired elements above (antero- and postero-supra-gnathals). The functional margins of these elements operate like a pair of shears with sharp edges, and in *Dinichthys* and its later allies, the anterior portions are provided with fang-like processes of great strength which interlock in biting. Rows of small denticles also occur on the gnathal elements in many Arthrodires. Sometimes, these run

¹ H. C. Stetson, "Notes on the Structure of *Dinichthys* and *Macropetalichthys*," *Bull. Mus. Comp. Anat.*, Vol. LXXI, 1930, No. 2.

along the entire length of the functional margins of the biting plates, as in *Dinichthys hertzeri* and *Diplognathus mirabilis*, while in other forms the denticles are present only on the symphysis and behind the cutting blades of the infero-gnathal and postero-supra-gnathal.

As long ago as 1844 Agassiz investigated the minute structure of a denticle of *Coccosteus* and found it to consist of vascular dentine, while in 1925 Stensio found the denticles on an arthrodiran jaw from Spitzbergen to consist of dentine and enamel.

Still later, D. Obruchev¹ described and illustrated the minute structure of the mandibular denticles in *Coccosteus trantscholdi*. He found that the teeth are not merely prongs of the jawbone, but consist of typical osteodentine and cement.

Other authors including Pander, Clappole, Jaekel, Dean, Hussakof and Stetson are unanimous in affirming that no dentine or enamel occurs in the jaw elements of the *Arthrodira*.

In 1931 Anatol Heintz² described and illustrated cross-sections, at various levels, through the denticles on the lower jaw of *Coccosteus decipiens*. He agrees with Obruchev that the denticles of *Coccosteus* consist of two dissimilar portions. The central and basal portion consists of true bone tissue. The peripheral portion is formed of a tissue that no longer shows the typical bone structure, but resembles osteodentine. Nevertheless, Heintz maintains that we cannot consider this latter tissue as typical dentine since no pulp and no fine parallel running canals are found. He agrees with Clappole and Moodie in believing that the teeth of the *Arthrodira* show a transition stage between true bone tissue and true dentine. According to Heintz no enamel is present in the denticles.

Some years ago I made a study of the histologic structure in the denticles of various Arthrodires, and, as this matter is of considerable importance, I shall describe some results of my investigations.

¹D. Obruchev, "Über *Coccosteus trantscholdi* (Eastman)," *Travaux du Musée Géologique près l'Académie des Sciences de l'U.S.S.R.*, t. VIII, 1929, p. 285-310.

²Anatol Heintz, "Untersuchungen über den Bau der Arthrodira," *Acta Zoologica*, Bd. 12, Stockholm, 1931.

In the first place, I found that true bone forms the substance of the jaw elements in all forms studied, excepting, however, denticles in certain species. It is in *Coccosteus*, as the most primitive Arthrodire in which jaw elements have been found, that we might expect to find true teeth, if they had ever been present in the Arthrodires. Accordingly, in a specimen of *Coccosteus decipiens* from Cromarty I found denticles exhibiting a modified dentine almost exactly as described by Agassiz.

There is no pulp cavity in the tooth. Its base is seated upon a layer of spongy bone with typical Haversian canals and lacunæ (Pl. I). Laterally to the base of the tooth, a sheath-like supporting layer of dense, modified bone with few canals, but many lacunæ, gradually merges into the denticle. The lacunæ become fewer in number as the denticle extends upwards and almost or quite disappear in the main body of the tooth. Vascular canals, arranged in three or four series, penetrate the tooth parallel with its longitudinal axis, and from these fine dentinal tubules extend to the outer surface (Pl. II). I find no evidence of enamel in my sections. Thus we have in *Coccosteus decipiens*, basally a modified bone substance transformed into vaso-dentine above.

In *Stenognathus mixeri*, from the Portage shales (Upper Devonian) of Western New York, denticles are found along the oral margins of both upper and lower jaw elements. In a thin section of one of these denticles from the mandible, the tooth is seen to be sharply differentiated from the supporting bone surrounding the base (Pl. III). Fine tubules radiate to the periphery from a central pulp cavity or canal. Some of these tubules resemble greatly elongated lacunæ. No Haversian canals are to be found in the denticle.

The species *Dinomylostoma buffaloensis* is founded upon certain Arthrodire mandibles from the Genesee (Upper Devonian) formation of Western New York. These mandibles represent a transitional stage between the knife-like cutting blades of *Dinichthys* and the crushing tritoral type found in *Mylostoma*. As many as six or eight symphysial denticles

are found on the mandibles of this species. Usually these denticles are worn down to their bases and the ridge upon which they lie is polished as if by functional wear.

A thin section of the base of one of these denticles (Pl. IV) shows an abrupt change from the enclosing bone, with its Haversian canals and numerous lacunæ, to an exceedingly hard dentine, with no canals and only a very few lacunæ. The fine tubules seem to radiate downwards from a focal point above, which may have been a small pulp cavity now destroyed by wear, as found in *Stenognathus*. A second denticle preserved in the section shows the same ankylosis to the base and the change from true bone to dentine is quite abrupt. A few lacunæ are found in the base of the denticle, but vascular canals are entirely absent.

Coccosteus canadensis is a fairly large fish from the Upper Devonian of Scaumenac Bay, Quebec. In this species the robust jaw elements are often well preserved and can be removed entire from the matrix. Specimens are rare, however, and I therefore illustrate on Pl. V, the nearly complete jaw elements of a single individual, in inner and outer view, for comparison with those of the better known *Dinichthys*.

Symphysial denticles appear to be absent on the infero-gnathal, but one or more stout denticles appear at the hinder end of the oral margin. No denticles are found on the antero-supra-gnathal, but on the postero-supra-gnathal two rows are seen. One row passes diagonally downwards and forwards across the lower exerted portion of the outer face of this element at about its middle; the other row, in which the denticles are shorter and not so conical, is situated on the hinder end of the element, directly behind the blade-like oral margin. This arrangement of denticles in a double row is exactly duplicated in the postero-supra-gnathal of *C. transcholdi* from the Upper Devonian of Northwest Russia.

A thin section of a denticle taken from the side of a postero-supra-gnathal (Pl. VI) shows a structure quite different from that of the more ancient *C. decipiens*. The substance of the denticle is a modified compact bone with few

canals and numerous lacunæ. There is a lamellar structure of the bone, and the lamellæ are arranged parallel to the long axis of the denticle. Two kinds of cell spaces are to be seen in the section, one kind typical lacunæ, their long axes parallel with the lamellæ, the other type consisting of elongated tubules disposed at right angles to the lamellæ. They are of a size and length to resemble dentine tubules, but are not so numerous as in typical dentine. We have here, perhaps, a variety of osteodentine.

Dinichthys (Gorgonichthys) clarkii possessed the largest and most powerful jaws of any known species. The animal, probably, represented the culmination of the predatory Dinichthyids of Upper Devonian time. The enormous mandibles of this species contain a few denticles at the posterior end of the oral margin. A thin section of one of these denticles shows that it was formed entirely of modified bone. The Haversian canals are very small and there are no traces of concentric lamellæ about them. The lacunæ are distributed in thinly scattered groups and there is no circular arrangement of them about the canals. This structure persists throughout the denticle to its tip (Pl. VII).

As a result of these studies I assume that the most primitive Arthrodires were equipped with functional teeth similar in origin to those of Gnathostomes. I also assume that the bony jaw elements were not originally provided with shearing edges and fanglike processes, but were supporting bones for functional teeth which, later, became obsolete. In the course of their evolution, an auxiliary biting mechanism may have been developed by means of a greater freedom of movement in lifting the head and this mechanism became more and more effective in the later predatory types. Coincidentally, the teeth were discarded and the supporting bones of the oral margin became functional as shearing organs. Still later, bony toothlike fangs were developed. The cutting margins of naked bone thus functionally transformed, of course were not, and could not, have been formed of dentine, but simply became more compact in response to the increased friction.

Finally, until more evidence is forthcoming, I presume the *Arthrodira* to have been true, if highly specialized, fishes, perhaps, in the remote past, having branched off from the Elasmobranch stem. Among them, of course, are included the *Acanthaspida*.

Genus *Euryaspis* Bryant

More than a dozen head-roofs and a large number of detached trunk-plates referable to this genus were collected by Dr. Dorf's party in 1932. Some of these are comparatively uncrushed. A few are preserved in counterpart. Unfortunately, only in one or two instances are plates of the trunk armor so associated as to afford reliable evidence that they belonged to one individual. It is now clear that two or three species of *Euryaspis* are present in this formation and, as in size and ornamentation, they are quite alike, it is at present hardly possible to refer certain detached plates to a particular species. Thus we have a number of cranial roofs, dorsal shields and antero-ventro-lateral plates obviously belonging to various species, but in the absence of associated parts of one individual the elements of a particular species can hardly be assembled.

To add to this difficulty, the bones of the cranial roof in *Euryaspis* are so completely fused that only in a few specimens can their outlines be determined, and, in distinguishing between them, one is forced to rely upon the general shape of the head-roof. Accordingly, it should be understood that the restorations of the dorsal and ventral armor of *Euryaspis*, as presented in Text Figs. 1 and 2, were based upon uncrushed detached plates of such size and shape that their overlapping margins exactly matched.

A very remarkable feature, unknown in any other *Arthrodira*, is the presence of a paired sensory canal in the orbital region in the head roof of *Euryaspis*. It is found in all of the crania examined where that region is well preserved.

Euryaspis brachycephalus Bryant

Pl. VIII, Figs. 1-3; Pl. IX, Fig. 2; Pl. X, Figs. 1, 2, 3, 5, 6;
Pl. XI, Figs. 1, 3, 4; Text Figs. 1, 2

Several head shields have been found in which the sutures between the various plates are quite apparent and the best of these are illustrated in Pl. VIII, Figs. 1, 2. It is, therefore, now possible to offer a more accurate sketch of the head-roof (Text Fig. 1) than that previously published.¹ In describing

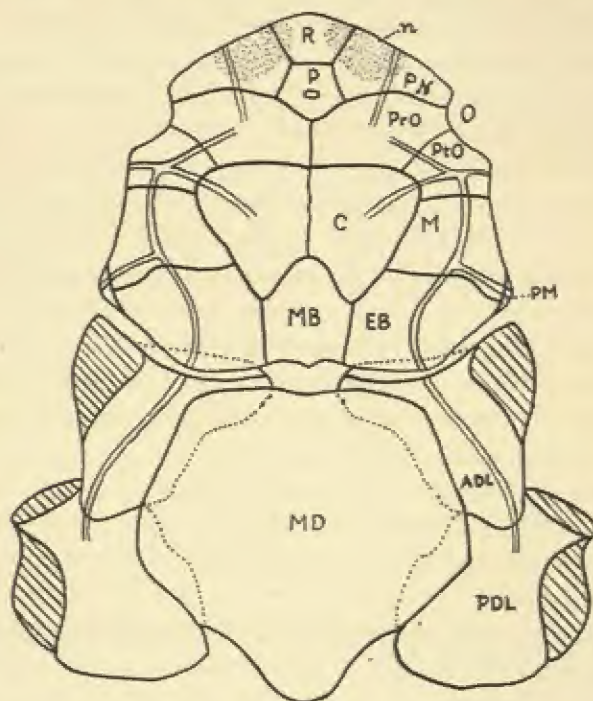


FIG. 1. *Euryaspis brachycephalus* Bryant. Plan of head-roof and dorsal armor. Sensory canal system shown as double lines. ADL, antero-dorso-lateral; C, central; EB, externo-basal; M, marginal; MB, median basal; MD, median dorsal; n, narial sacs; O, orbit; P, pineal; PDL, postero-dorso-lateral; PM, post-marginal; PN, post-nasal; PrO, pre-orbital; PtO, post-orbital; R, rostral. Ca. $\times 2$.

this and other forms, I adopt the revised nomenclature lately agreed upon by Heintz and Hyde for the plates in the *Arthrodira*.

¹ Bryant, W. L., Proc. Am. Phil. Soc., Vol. LXXI, No. 5, p. 244, Fig. 5, 1932.

It is clear that the median basal plate is narrower behind and more truncated in front than I had supposed. It is thus seen to resemble closely the corresponding bone in European forms. The limits of the externo-basal bone can be distinguished in certain specimens, but the suture between the marginal and post-orbital plates is entirely obliterated in every specimen I have examined.

I am convinced that a small post-marginal bone was present in *Euryaspis*, for the reason that certain head shields are extended into a pronounced angle in this region, while in other specimens the posterior lateral angle of the head-roof is rounded as though this bone had broken away, a condition often found in *Coccosteus*.

The rostral plate is small, not much larger than the pineal. It is flanked on each side by a large, wide plate which also forms most of the lateral boundary of the pineal plate and extends to the lateral margin of the head-roof, taking a small part in the boundary of the orbit. The pre-orbital sensory canal crosses this plate. In accordance with the nomenclature proposed by Heintz I call this element the post-nasal bone. It is evidently homologous with a similar plate in *Phlyctenaspis acadica*, first made known by Woodward and called by him the pre-maxilla. Some specimens show that the post-nasal bone was vaulted over the narial sac (Pl. IX, Fig. 2), but there is no distinct narial notch on the anterior margin of the head-roof.

The pineal plate, where well defined, is seen to be a rather large polygonal bone, in which the pineal pit is usually conspicuous. In some forms this plate is much smaller and oval in shape. The pineal pit, apparently did not open above. Of the side plates of the head, only fragments of the sub-orbital have been found. The eye was large and a sclerotic ring was present. An impression of a portion of this ring is to be seen on the specimen figured on Pl. IX, Fig. 2. It was, apparently, composed of more than four separate bones which is the usual number found in the *Arthrodira*.

The sensory canal system in *Euryaspis* corresponds to

that in other Acanthaspids with the following exceptions. The pre-orbital canal, arising on the pre-orbital plate, crossed the post-nasal plate to terminate on the front margin of the head. A canal, not hitherto found in the *Arthrodira*, but apparently an extension of the marginal canal, arises at or near the junction of the latter with the post-suborbital canal and passes forward above the orbits nearly to the posterior end of the pre-orbital canal. In its course, it traverses both the post-orbital and pre-orbital plates. I propose to call this the pre-marginal canal. Nothing is known of the jaws or dentition in *Euryaspis*.

As in all other *Arthrodira* the head was no doubt movably articulated to the antero-dorso-lateral plates on the trunk carapace. The connection, however, must have been of the simplest type. There are no traces to be seen of a fossa glenoidalis on the externo-basal plate and no condyle on the antero-dorso-lateral plate. The posterior margin of the externo-basal plate overlapped the anterior margin of the antero-dorso-lateral plate where it was received in a shallow groove.

The median dorsal plate is separated from the head-roof by a considerable gap. It is strongly arched from side to side and from front to rear, and bears on its centre a pronounced node. Only the faintest trace of a keel is to be seen on the visceral surface. This surface also shows along the lateral borders the impressions of the articulating areas of the antero-dorso-lateral and postero-dorso-lateral elements which it overlapped (Pl. X, Fig. 2). The median dorsal plates in the collection vary considerably in outline and probably more than one species is represented (Pl. X, Figs. 1, 4).

The antero-dorso-lateral plate is quite narrow in the exposed surface, but bears wide margins of overlap. Its upper anterior process intervenes between the median dorsal plate and the head-roof (Pl. XI, Fig. 1).

The postero-dorso-lateral plate is wider behind than in front, is traversed for a short distance by a lateral line, and was apparently overlapped by four elements, the median dorsal, the antero-dorso-lateral, the antero-lateral, and the

postero-lateral. The latter plate has not yet been recognized, but it must have been present as shown by an area of overlap on the lateral margin of the postero-dorso-lateral (Pl. X, Fig. 5).

The antero-lateral plates in the collection vary to some extent in shape and probably more than one species is represented. Its lower margin embraces the spinal plate. The plate is strongly arched from front to rear. The visceral surface is smooth with no pronounced keel. On Pl. XI, Figs. 2 and 3, I show two forms of this element, one in inner, the other in outer view.

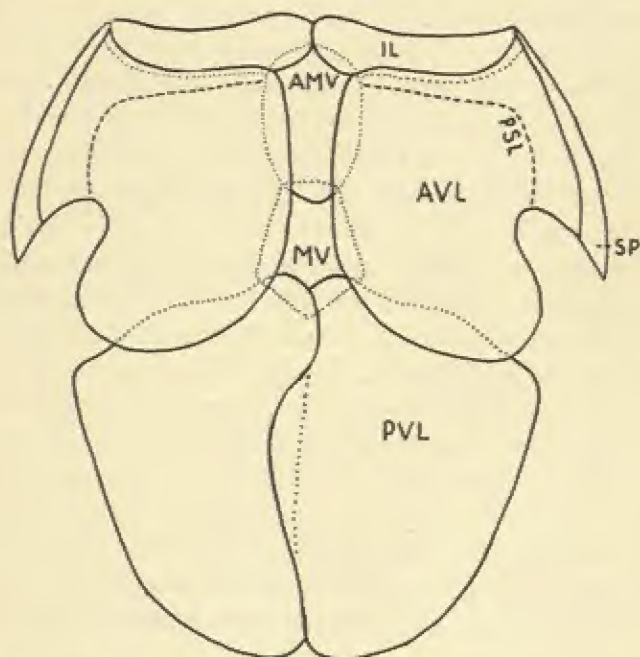


FIG. 2. *Euryaspis brachycephalus* Bryant. Plan of ventral armor. AVL, antero-ventro-lateral; AMV, antero-median-ventral; IL, inter-lateral; MV, median ventral; PSL, pre-spinal lamella; PVL, postero-ventro-lateral; Sp, spine. Ca. $\times 2$.

In Text Fig. 2, I have drawn a reconstruction of the ventral armor. This is partly based upon the specimen illustrated on Pl. XI, Fig. 1, one of the few instances in which a number of plates, evidently belonging to the same individual, are

grouped together. As seen in this specimen, the impression of the intero-lateral plate extends across the front margin of the antero-ventro-lateral. It seems to have consisted of two wings as in *Coccosteus*. In most specimens examined the bone has become detached, exposing the recess in which it formerly lay. In some cases it was in contact with its fellow in the median line of the fish. In others it is slightly separated by an intervening process of the antero-median-ventral. At the outer end, it was apparently in contact with the spinal plate.

The antero-ventro-lateral plate is arched very gently from side to side in front, but behind the spine its postero-lateral area is strongly flexed upwards and here the plate may have come into contact with the postero-dorso-lateral element of the dorsal shield. In advance of this area, the lateral margin of the antero-ventro-lateral is gently arched and overlaps the spinal plate.

On the visceral surface of the antero-ventro-lateral plate, a thin keel or lamina of bone, the "pre-spinal lamina" of Heintz, curves around the plate as indicated by dotted lines in the sketch (Fig. 2, PSL).

The spinal plate for most of its length is firmly fixed between the outer margins of the antero-lateral above and the antero-ventro-lateral below. The outer margin of the spine is ornamented with a row of enlarged tubercles. The posterior free margin carries a series of minute denticles. The distal end of one of these spines is shown enlarged on Pl. XI, Fig. 4.

The postero-ventro-lateral plate is gently arched from side to side. Seen from below the right postero-ventro-lateral overlaps its mate of the left side, and is itself overlapped by the antero-ventro-lateral. The antero-median ventral plate is long and narrow (Pl. VIII, Fig. 2), and overlaps the anterior end of the median ventral. The latter (Pl. X, Fig. 6) is a diamond shaped plate with margins of overlap on all sides.

The posterior part of the trunk of *Euryaspis* was covered with scales, but nothing is known of its shape or of its fins, and only detached scales have been found.

Euryaspis obscurus n. sp.

Pl. IX, Fig. 1; Text Fig. 3

Type: A cranial shield in yellow limestone (No. 13577).

The type and only specimen of this species is distinguished by very large eye-notches and pointed snout. The cranial roof, as preserved, is well vaulted, especially in front. The postero-lateral contours are angular. The component bones of the head are so firmly fused that little can be seen of their outlines. In the orbital region, one sees the beginnings of the sutures that form the boundaries of the pre-orbital plates. These, for some reason, are always conspicuous in *Euryaspis* heads. Most of the upper margin of the orbit must have been formed by the post-orbital plate, for the anterior and posterior sutures of the pre-orbital plate seem to meet at the orbital notch, thus excluding the pre-orbital plate from the orbit.

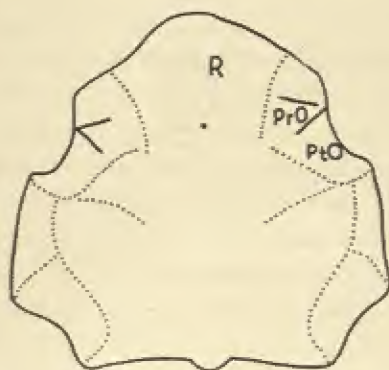


FIG. 3. *Euryaspis obscurus* n. sp. Outline of head-roof with sensory canal system. PrO, pre-orbital; PtO, post-orbital; R, rostral. Ca. $\times 2$. Based on type specimen, No. 13577.

The total length of the head-roof is 29 mm. and its extreme width is 30 mm. The pineal impression is far back. The sensory canal system is well preserved, and is like that in *E. brachycephalus*. The pre-marginal canal is present, but is not a direct continuation of the marginal canal. The bones are ornamented with fine tubercles.

No doubt certain detached plates of the body carapace in the collection pertain to this species, but it is at present impossible to confirm it.

Euryaspis cristatus n. sp.

Pl. XII, Figs. 1-3; Text Fig. 4

Type: A dorsal shield imbedded in yellow limestone (No. 13731).

Dorsal shield somewhat wider than long, emarginate in front, pointed behind, strongly arched from side to side and from front to rear. A longitudinal, median row of stout denticles extends from the posterior end of the shield to the median node. Here they become greatly enlarged, forming a crest composed of four or five compressed, spine-like teeth. Ornament consisting of fine, pear-shaped tubercles.

Several more or less fragmentary shields belonging to this species are found in the collection. Of these, perhaps the best is the type (Pl. XII, Fig. 1). The specimen is preserved mostly as an impression with a certain amount of bone adhering. Only when imbedded with the visceral side upwards are the denticles preserved. A portion of the lateral margin of each side has been broken away on the type specimen. A more complete shield is shown on Pl. XII, Fig. 2, and the median row of denticles is seen on the posterior half of a fragmentary specimen illustrated on Pl. XII, Fig. 3. The type specimen measures 29 mm. in length and was originally somewhat wider than long.

Euryaspis spec. indet.

Detached plates from the ventral armor are abundant in the collections from Beartooth Butte. These, obviously, represent several species, probably one or another of those above described. Pending the discovery of associated remains, I content myself with illustrating the most divergent forms on Pl. XIII, Figs. 1 to 6. The specimen shown on Pl. XIII, Fig. 2 is the only one in which I have found the intero-lateral element preserved in place.

In many respects, *Euryaspis* is closely related to the German species described as *Acanthaspis heintzi* by Gross. In both, the head plates are firmly fused, while the trunk armor is divided, with broad areas of overlap. In both, the median dorsal plate is very wide and strongly arched in all directions, while the median keel on the visceral surface is exceedingly feeble. In both, a postero-lateral plate separates the postero-dorso-lateral from the postero-ventro-lateral.

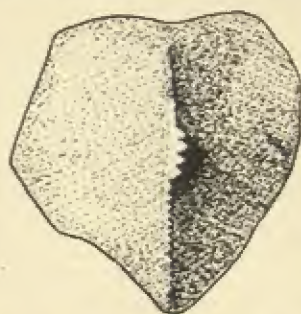


FIG. 4. *Euryaspis cristatus* n. sp. Median dorsal plate. Ca. $\times 1\frac{1}{2}$. Based on No. 13710 with details from other specimens.

On the other hand, the head-roof in *Euraspis* is shorter and wider, a large post-nasal plate is present, and the sensory canal system differs in some important features. The antero-dorso-lateral plate is narrower in *Euryaspis* and the condyle seems to be wholly absent. It is also evident that *Acanthaspis heintzi* must be assigned to a new genus since the antero-ventro-lateral plates are obviously very different from those of the type species.

Genus *Anarthraspis* n. gen.

Acanthaspids with head broader than long, well arched from side to side, narrow in front, but with strongly developed lateral lobes. Orbits small and placed far forwards. Rostral plate large. Fossa glenoidalis of the externo-basal plate and condylus glenoidalis of the antero-dorso-lateral plate feeble or absent. Membrane bones ornamented with tubercles. Jaw elements unknown. Head plates, excepting in the rostral region, firmly fused. Trunk armor divided. Two species are known.

Anarthraspis chamberlini Bryant

Pl. XIV, Figs. 1-3; Pl. XV, Figs. 1, 3; Pl. XIX, Fig. 2; Pl. XXIV, Fig. 3; Text Fig. 5

1932. *Coccosteus chamberlini* Bryant. Proc. Amer. Phil. Soc., Vol. LXXI, No. 5, p. 250, Pl. IX, Figs. 2, 4.

This species was founded upon certain detached plates of the trunk carapace and upon a fragment of the head shield. These were thought by the present writer to pertain to a new *Coccosteus*. Since then, six more or less complete head shields have been found and a number of plates from the trunk armor. Together they demonstrate beyond question that we are here dealing with an *Acanthaspis*.

Viewed from the upper side, the head-roof is seen to be closely studded with minute tubercles. The rostral region is usually broken cleanly away exposing its suture line, but in the only specimen in which it is preserved in place that suture, like all others of the head-roof, is completely obliterated. The only exceptions to this are short paired suture lines in the orbital region marking the division between the pre- and post-orbital bones.

Viewed from below, the bones are also completely fused together. The visceral surface of the head-roof is remarkably smooth, although low ridges and shallow depressions are found, corresponding in general to those of *Coccosteus*.

The shape of the head-roof can be seen by examining the specimens figured on Pl. XIV, Fig. 1; Pl. XV, Fig. 1. In both of these, however, the rostral plate is missing. A detached rostral plate, perhaps belonging to a juvenile individual of this species, is illustrated on Pl. XXIV, Fig. 3. It shows areas of overlap. In certain specimens ossification rays of the bones in the head are fairly well preserved and have made possible the restoration of the head-roof shown in Text Fig. 5. The pineal plate has not been found.

The eye notches are small and located far forward. However, the rostral plate takes no part in the upper contour of the orbit, this being formed by margins of the pre-orbital and post-orbital plates.

There are no traces of a fossa glenoidalis on the externo-basal plate in any specimen before me. This element overlapped the antero-dorso-lateral to a considerable extent. The connection between the two is of the simplest type as com-

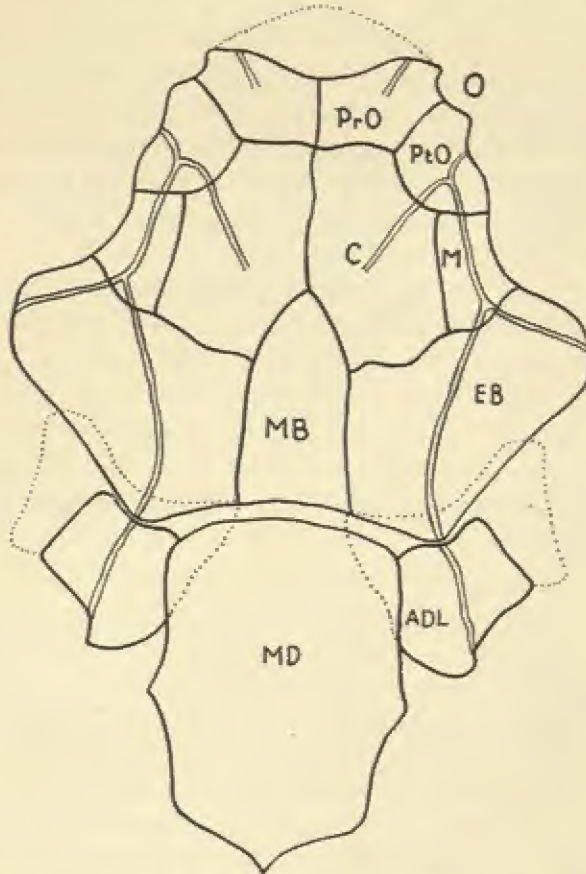


FIG. 5. *Anarthraspis chamberlini* Bryant. Plan of head-roof and dorsal armor. ADL, antero-dorso-lateral; C, central; EB, externo-basal; M, marginal; MB, median basal; MD, median dorsal; O, orbit; PrO, pre-orbital; PtO, post-orbital; R, rostral. Ca. $\times \frac{1}{6}$.

pared with other Arthrodires, and it is questionable how much independent motion could have been exercised by the head. Certainly there were no robust seats of attachment for muscles such as are found on the under sides of the head-roof in *Cocosteus* and *Dinichthys*.

The sensory canal system forms open grooves on the upper surface of the head-roof. On the under surface of the head these canals are often visible because the bone is thickened or depressed along their course. There is no pre-marginal canal such as is seen in *Euryaspis*. The pre-orbital must have traversed a post-nasal plate. Otherwise the canal pattern agrees well with that in other Acanthaspids.

Of the trunk armor the following plates are known: median-dorsal, antero-dorso-lateral, intero-lateral, antero-ventro-lateral, spinal, antero-median-ventral, and median ventral. Some of these are illustrated on Pl. XIV and Pl. XV. It will be seen that only the merest rudiment of a condyle appears on the antero-dorso-lateral plate (Pl. XIV, Fig. 2). It is also to be observed that a broad region across the entire anterior margin of the ADL was overlapped by the head.

The median-dorsal plate is represented by a fragment showing the right half of the plate in visceral aspect (Pl. XIV, Fig. 3). There is no trace of a median keel and probably none existed. While this plate must have been longer than wide, another median-dorsal plate in the collection belonging to this or another species is broader than long (Pl. XIX, Fig. 2).

The intero-lateral plate is a long narrow bone, shaped as in *Euryaspis*. The antero-ventro-lateral plate was about as broad as long (Pl. XV, Fig. 2). Only the anterior portion of the spinal is known, but its free end probably did not extend beyond the end of the antero-ventro-lateral. A right postero-ventro-lateral plate, apparently of this species, is shown on Pl. XV, Fig. 3. The antero-median-ventral and median ventral plates are similar to those of the next species to be described, but smaller.

The tail of this fish was no doubt covered with scales, but nothing is known of its shape or of the fins. No traces of the jaw elements have been found, and I must say here that the specimens illustrated as supposed infero-gnathal and postero-supra-gnathal elements described in a former paper as of *Coccosteus chamberlini* were no doubt misinterpreted as jaw

elements. The specimen regarded as a postero-supra-gnathal is in fact a postero-ventro-lateral plate of a juvenile *Euryaspis*. The mandibular element, if such it is, may not pertain to an Arthrodire.

Anarthraspis montanus Bryant

Pl. XVI, Figs. 1-3; Pl. XVII, Figs. 1, 2; Pl. XXIV, Fig. 2;
Text Fig. 6

1932. *Svalbardaspis montanus* Bryant. Proc. Amer. Phil. Soc., Vol. LXXI, No. 5, p. 249, Pl. X, Fig. 1.

1932. *Coccosteus chamberlini* Bryant. Proc. Amer. Phil. Soc., Vol. LXXI, No. 5, p. 251 (antero-dorso-lateral plate), Pl. IX, Fig. 1.

This species was founded upon a detached rostral plate resembling the same element in *Svalbardaspis*, a form from Spitzbergen, and provisionally placed in that genus by the present writer. Since then three or four nearly complete heads have been found. These show that we are dealing with a second and larger species of *Anarthraspis*, a genus peculiar to the United States. As in *Svalbardaspis stensiöi*, the rostral plate forms most of the anterior margin of the head-shield, and the orbits are small and placed far forward, but the shape of the head is very different from that of *Svalbardaspis*, being much wider and more angular in the posterior half.

The head, Text Fig. 6, is large and well arched. It measured about 132 mm. in length by 142 mm. in greatest width, and thus is wider than long. The rostral plate is detached in all specimens known to me, but the other plates of the head-roof are fused and their boundaries difficult to ascertain. The large rostral plate has already been described, but the pineal plate is unknown. A reexamination of the so-called pineal plate in the type specimen convinces me that it is only a peculiar fracture in the visceral surface of the rostral plate. The pre-orbital plates are long and are in contact with each other in the median line. The post-orbital plate is small. The marginal plate is long and narrow in front and

throughout its length is in contact with the central plate. The median basal plate is long, with straight sides. A short projection is found on the posterior end of this plate in the median line as in many other *Arthrodires*. There is no trace of joint sockets on the externo-basal bones.

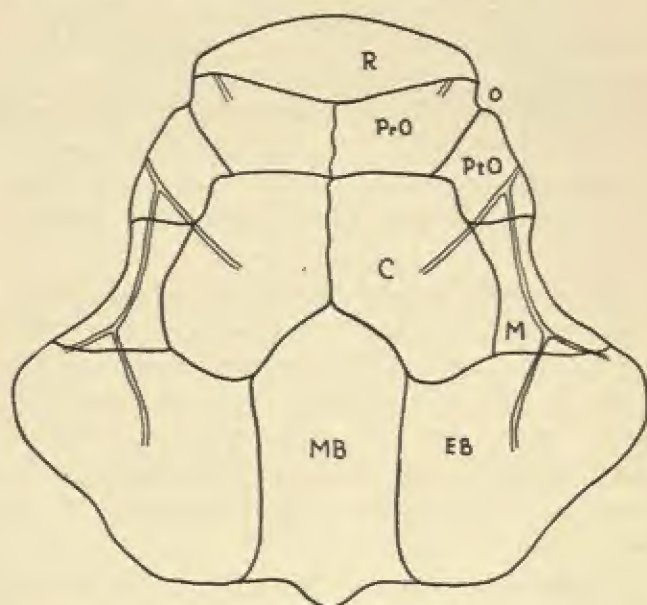


FIG. 6. *Anarthraspis montanus* Bryant. Plan of head-roof. C, central; EB, externo-basal; M, marginal; MB, median basal; O, orbit; PrO, pre-orbital; PtO, post-orbital; R, rostral. Ca. $\times \frac{3}{8}$.

All of the heads in the collection are badly weathered. The most complete specimen (Pl. XVI, Fig. 1) is preserved as an impression of the visceral surface. Other examples show that the outer surface was ornamented with small stellate tubercles. On the trunk plates these tubercles are somewhat larger. The sensory canal system is like that in *A. chamberlini*. The pre-orbital canal certainly must have crossed over onto a post-nasal plate as shown by several examples. The side plates of the head are unknown.

Of the trunk armor, the antero-dorso-lateral plate has already been described. The other plates of the dorso-lateral armor have not been identified. There is no condyle on the

antero-dorso-lateral plate, but a long area of overlap on its anterior margin. This area forms a groove into which the externo-basal plate of the head must have fitted, exactly, as in *A. chamberlini*. There are also wide areas of overlap to receive the median dorsal and the antero-lateral plates.

All of the plates composing the ventral shield are known from isolated specimens. The antero-median-ventral and median-ventral are illustrated on Pl. XVI, Figs. 2, 3, and need no detailed description. The antero-ventro-lateral (Pl. XVII, Fig. 1) is about as long as wide. A portion of the spinal and most of the intero-lateral plates are preserved with the specimen illustrated. It will be observed that the spinal element was short and its distal extremity did not extend so far as the posterior end of the antero-ventro-lateral. The latter plate is nearly flat, but its postero-lateral margin is strongly flexed upwards. The postero-ventro-lateral plate is known by a number of imperfect specimens. One of these (Pl. XVII, Fig. 2) shows that the outer margin of the plate was also strongly curved upwards, following the contour of the antero-ventro-lateral which overlapped it. The plate is long and narrow.

Nothing has been found of the jaw elements in this species with the possible exception of a small fragment of bone bearing a row of toothlike denticles on one margin. This bone is shown enlarged on Pl. XXIV, Fig. 2. As there are distinct traces of a tubercular ornamentation on this bone, it possibly may be a portion of a spinal plate, the outer margin of which is still unknown.

Certain large, round, or oval scales bearing an ornamentation similar to that of the above described plates, probably are from the body of this fish.

Sub-Class ELASMOBRANCHII. ICHTHYODORULITES

Machaeracanthus minor n. sp.

Pl. XVIII, Fig. 1

Type: A complete spine in yellow limestone (No. 13664).

Spine small, slender, tapering, gently arched. Sides marked with a single longitudinal ridge. This is narrow and

sharp proximally, bounded by wide sulci on each side, and becomes broader and more rounded distally until it occupies most of the lateral surface of the spine. Inserted portion short.

Spines referred to this genus have been found in Lower and Middle Devonian rocks both in Europe and America. They are similar in character to the spines of *Acanthodes concinnus* Whiteaves from the Upper Devonian of Scaumenac Bay, Quebec, and no doubt the little spine here described belonged to an earlier Acanthodian fish.

Onchus peracutus n. sp.

Pl. XVIII, Fig. 3

Type: A small spine in red limestone (No. 13666).

Spine long, straight, acute, and slender with sharp edges. Pulp cavity extending to the apex. Sides ornamented with a median series of several sharp longitudinal ridges. Inserted portion short and finely striated.

The small but robust spine described herewith is known by a single specimen. Unfortunately this is badly crushed throughout its length, and the number of ridges on the exposed lateral surface cannot be determined. As it obviously differs decidedly from any other spine in the collection, I have given it a name, although the description must at present remain a little indefinite.

Genus *Pinnacanthus* n. gen.

Spines small, much laterally compressed, sigmoidal in outline. Sides ornamented with exceedingly fine, subparallel but undulating longitudinal striæ. Posterior margin with a single series of slender denticles directed upwards.

Pinnacanthus inequistriatus n. sp.

Pl. XVIII, Fig. 2

Type: A small spine in yellow limestone (No. 13665).

A small but graceful spine with slightly sigmoidal outline. Inserted portion long and tapering. Exposed portion much compressed. Ornament consisting of longitudinal striations

so fine that they are invisible to the naked eye. Slender denticles on posterior face directed upwards.

In some features this spine resembles *Bulbocanthus rugosus* Bryant from the same formation and locality. Both are greatly compressed, and are more or less sigmoidal in outline, with sharp upwardly directed denticles on the posterior face. Both are ornamented with wavy striæ. In *Pinnacanthus*, however, the striæ are much finer, and the base of insertion is very different. As the original illustration of the type specimen of *B. rugosus* was indistinct in some details, I figure another and more complete specimen much enlarged on Pl. XVIII, Fig. 4, for comparison with the present form.

Genus *Helenacanthus* n. gen.

Spines small, curved, laterally compressed and tapering. Pulp cavity large, extending to the apex. Sides of exerted portion ornamented with numerous smooth, longitudinal costæ. Posterior face with a single series of stout denticles. Base unknown.

Helenacanthus incurvus n. sp.

Pl. XIX, Fig. 1

Type: Two incomplete spines imbedded in red limestone (No. 13662).

The small, jaw-like elements upon which this species is founded are crushed and broken. As preserved, the largest spine measures about 40 mm. in length and 4 mm. in greatest width. One spine is strongly curved, the other less so, the latter probably being only the proximal portion of a spine. On the posterior face of each is to be seen a single row of stout, closely approximated denticles. The lateral faces are ornamented with numerous fine, smooth, longitudinal ridges. In neither specimen is the base preserved. It is evident that the distal half of the spine is much more curved than the proximal end.

INCERTÆ SEDIS

A large fragment of shagreen forming part of the integument of some unknown fish is shown on Pl. XX. The

shagreen consists of small polygonal granules with basal cavities. As seen by folds in the present specimen the integument was quite flexible. None of the granules are perfectly preserved. Whether the specimen pertains to a selachian or to an ostracoderm like *Thelodus* is uncertain.

Another specimen exhibiting the integument of most of the trunk of an unknown fish is illustrated on Pl. XXI. Here the trunk is seen to be covered with apparently smooth, ovoid scales. Head and fins are absent. What seems to be the tail of the fish is covered with scales. Adjacent to the specimen is a bone fragment which may belong to the head. This bone is ornamented by rows of fine punctæ forming a rugose surface.

PART III. SUPPLEMENTARY NOTES ON THE HETEROSTRACI

Shortly after the completion of the foregoing paper, there was forwarded to the author a small but exceedingly important collection of fossils gathered by Dr. Dorf and his party at Beartooth Butte during the summer of 1933. Included are two Protaspids exhibiting the trunk behind the armor and, in one of these, the forepart of the tail is preserved. The collection also includes a dorsal shield of a form representing a new genus and species belonging in the primitive family *Poraspidae* among the *Heterostraci*, and a large Merostome described by Dr. Ruedemann, in a brief paper appended hereto, as *Pterygotus princetonii*. The discovery of a Eurypterid in the Beartooth Butte fauna is of special interest because they are found in association with Acanthaspids, which come closest to those here described, in the Lower Devonian of Germany. Both *Pterygotus* and *Eurypterus* are there found in association with Acanthaspids, Cephalaspids and some Pteraspids. The Acanthaspids are very close to *Euryaspis*, but differ in some minor particulars.

The fish fossils are discussed herewith.

Protaspis bucheri Bryant

Pl. XXII; Pl. XXVI, Fig. 2

The unique specimen illustrated on Plate XXII shows dorsal and ventral shields crushed together. Behind these extends a slender and attenuated whiplike body covered with large scales. The tail of the animal was unfortunately broken away.

The fossil lies on its back with the ventral side uppermost. The branchial plates are still attached. The head is incomplete in the oral region and so badly crushed that nothing can be determined concerning the plates that surround the mouth. The ventral shield is closely superimposed upon the dorsal element and in many places has broken away. It is apparent that in life the hinder end of the carapace was constricted and formed a comparatively narrow opening through which the trunk projected. There is no evidence of cornual plates in the fossil. It seems certain that branchial outlets must have been located in this region.

The scales of the body behind the armor are badly crushed and broken. Nevertheless, they occupy their normal position. Apparently there was a median series of long, pointed scales both dorsal and ventral. Towards the posterior end of the trunk the scales remain comparatively large, and only two or three scales are contained in the depth of the body. The trunk is broken off just in front of the tail which, unfortunately, is missing.

Due to crushing the orbits are rarely preserved in Protaspid fossils. A fragment of a dorsal shield of *P. bucheri* has been found in which one orbit is perfectly preserved. I illustrate this on Pl. XXVI, Fig. 2.

Protaspis dorfi Bryant

Pl. XXIII; Pl. XXIV, Fig. 1

Another specimen of a Protaspid in which portions of the body behind the armor have been found is illustrated on Pl. XXIII. Here we have the dorsal shield preserved in outer aspect, and crushed flat. At the point where the body pro-

jects beyond the armor the fossil, unfortunately, has been fractured and a portion destroyed. However, the two blocks fitted perfectly below the fossil and as repaired the tail lies exactly in its original position.

In this case the proximal moiety of the tail is also preserved. As in *P. bucheri* the body behind the armor is slender and defended by median dorsal and ventral series of large, pointed scales with a few lateral scales intervening. Approaching the tail the lateral scales become smaller and more numerous, extending into the tail itself (Pl. XXIV, Fig. 1). The tail was either truly heterocercal, or of the reversed heterocercal type known as hypocercal. The fulcral scales rapidly diminish in size on the tail portion.

The trunk is comparatively much shorter than in *P. bucheri*, and it should be observed that the reconstruction of this fish presented on Plate III, Part I of this paper is incorrect in so far as the trunk in front of the tail is concerned. The trunk is now known to have been much more slender and whip-like, and the sides of the dorsal shield converged posteriorly conforming to the shape of the slender trunk.

Cyrtaspis papillatus Bryant

Pl. XXV

Among the specimens collected during the past summer is a fine large, uncrushed dorsal shield of *Cyrtaspis papillatus*. As this specimen is much more complete than the type, I have illustrated it on Pl. XXV. The shield is little deformed by crushing except for the branchial plates and was steeply arched. The height of the arch in the dorsal shield, at about the centre of the first year's growth as shown by growth rings, was about 22 mm. *Cyrtaspis* was therefore a comparatively deep-bodied fish. Normally, the hinder portion of the shield was much constricted and the trunk behind the shield must have been slender as in *Protaspis*. The sensory canal system is shown in part on this specimen and agrees well with that in other members of the family.

If the conspicuous concentric rings or annuli on the cara-

pace of the specimen are due to yearly cycles of growth, then this individual must have been about eight years old at death.

Genus *Cryptaspis* n. gen.

Comparatively large forms belonging in the family *Poraspidae*. Dorsal shield entirely undivided and weakly vaulted. Rostral region broad, unconstricted. Maxillar brim apparently undeveloped. Lateral lobes weak. Post-branchial portion rather long. The dorsal shield terminating posteriorly in a short, rounded, median lobe. Orbital notches small. Pineal and branchial impressions weak. Brain impressions absent. Branchial plate oblong, always detached, but showing areas of overlap. Dermal skeleton with well developed cancellous layer. Dentine ridges fine, flat on top, but laterally crimped. Sensory canal system similar to that in *Poraspis*.

The presence of a number of species of this genus in the Beartooth fish beds is indicated by a goodly number of detached branchial plates of variable size and shape. Some of these are nearly straight while in others the lateral margin is strongly concave in outline on one side and convex on the other. The complete branchial plate of a rather large form was illustrated in a former paper¹ as a supposed branchial plate of *P. bucheri*, and a fragment of a large dorsal shield doubtless belonging in this genus is noticed in Part I of the present paper (Vol. LXXII, No. 5, 1933, p. 312) and illustrated on Pl. XVII, Fig. 2. However, the only definable species is based upon the unique fossil described below

Cryptaspis ellipticus n. sp.

Pl. VIII, Fig. 4; Pl. XXVI, Fig. 1; Text Figs. 7, 8

Type: A complete dorsal shield in red limestone (No. 13752).

Dorsal shield semi-elliptical in outline and undivided, with weak branchial lobes. Orbits small and directed laterally. Pineal macula and branchial impressions indistinct. Maxillar brim apparently undeveloped. Branchial plates oblong with

¹ W. L. Bryant, "Lower Devonian Fishes of Beartooth Butte, Wyoming," *Proc. Amer. Phil. Soc.*, Vol. LXXI, No. 5, 1932, p. 237, Pl. III, Fig. 3.

subparallel sides. Sensory canal system like that in *Poraspis*. Dentine ridges flattened, with crimped sides. Arranged fan-shaped on the rostral and post-branchial areas. Elsewhere running in subparallel, longitudinal rows separated by minute grooves. Five of these ridges contained in 1 mm.

The only dorsal shield of this species which has yet come to light is illustrated on Pl. XXVI, Fig. 1, and a tracing of the fossil showing the lateral line system is presented in Text Fig. 7. The shield is only gently arched, perhaps due to crushing,



FIG. 7. *Cryptaspis ellipticus* n. sp. Outline of dorsal shield showing sensory canal system, several branchial impressions, and fragment of branchial plate. Ca. $\times 36$. Based on the type specimen, No. 13752.

and, as preserved, exhibits the cancellous layer throughout its extent, exposing most of the sensory canals. Nevertheless, the bases of the dentine ridges may still be seen and in one or two small areas they are completely preserved. I believe I have recognized a small orbital notch on one side. The pineal macula may be seen, although indistinct, and three weak

branchial impressions are preserved on one side. On the other only one can be seen. Impressions of nasal sacs and of semi-circular canals are absent. A considerable portion of the right branchial plate lies adjacent to the shield, but little moved from its normal position. There is no indication of the position of the branchial opening on any of the detached branchial plates in the collection, but this orifice probably was located on the upper margin of the branchial plate and in advance of the lateral lobe of the dorsal shield as in *Poraspis*.

The lateral line system is very distinct on the type specimen and a tracing of it is given in Text Fig. 7. With certain differences, it strongly resembles the lateral line system in *Poraspis polaris* Kiaer. The transverse commissures extend across the plate from one margin to the other. The V-shaped line, lying just behind the pineal macula, does not meet the outer longitudinal line as in *Poraspis*. There are also two other paired diagonal canals which are not found in the *Poraspids*.

A lateral fragment of a ventral shield, probably belonging to this species, is shown on Pl. VIII, Fig. 4. It exhibits quite clearly the lateral line system of that region. This appears to consist of two lateral longitudinal canals and a series of transverse commissures. The latter originate at the inner longitudinal canal and extend inwards for an unknown distance. Nine of these transverse lines are to be seen on the specimen (Text Fig. 8). The anterior and posterior transverse canals extend outwards, forming a connection between the paired longitudinal lines.

In all hitherto described *Pteraspids* and *Poraspids* only one longitudinal lateral line is found on each side of the ventral shield. I, therefore, closely examined this specimen to see if the outermost longitudinal line could be due to a fortuitous fracture. Along some portions of its length it certainly does resemble the impression of a fracture, but in other parts it seems clearly defined as a lateral line. Nothing is known of the squamation of the trunk behind the shield.

The nearest American relative of this primitive species is *Palaeaspis* from rocks of the Salina group of the Silurian in Pennsylvania.



FIG. 8. *Cryptaspis ellipticus* n. sp. (?). Fragment of ventral shield showing sensory canal. Ca. $\times \frac{3}{4}$. No. 13738.

CONCLUSION

The discovery and exploration of the Beartooth fish lens opened a new chapter in our knowledge of the long history of vertebrate evolution. It revealed another locality where, in Lower Devonian times, lay a body of water teeming with fishes. Already a surprising variety of animals has been described and it is certain that the list is by no means exhausted. Twenty-eight named species are now known from this lens, all of which are new to science. Several orders of vertebrates are represented, and among these, eight of the thirteen genera found here are new.

Discoveries like these help to fill in the wide gaps in the history of vertebrate evolution that are ever narrowing. Here we find a group of animals closely related to those found in former water pools of the same period as far away as eastern Europe, together with a few large, but highly specialized forms which seem to have arisen in America. On the whole, the fauna of Beartooth Butte differs from the European fauna

of the same period hardly more than do modern fishes from equally far separated waters.

A comparison of the Beartooth fauna with that of the Lower Devonian beds of Overath, Germany, discloses the following more or less closely related groups of genera.

BEARTOOTH BUTTE

OVERATH

HETEROSTRACI

*Protaspis**Cyraspis**Cardipeltis**Cryptaspis**Pteraspis**Drepanaspis*

OSTEOSTRACI

*Cephalaspis**Cephalaspis*

ARTHRODIRA

*Euryaspis**Anarthraspis**Acanthaspis**Leptaspis*

ICHTHYODORULITES

*Onchus**Machaeracanthus**Pinnacanthus**Bulbocanthus**Helenacanthus**Onchus**Machaeracanthus**Gyracanthus*

DIPNOI

Dipterus sp. (?)

MEROSTOMATA

*Pterygotus**Pterygotus**Eurypterus*

These discoveries also help to emphasize the fact that, in Lower Devonian time, vertebrates in great numbers and of widely different lineage had found their way half around the world, varying in response to a changed environment, and that a long and involved history lay behind them.

PRINCETON UNIVERSITY, PRINCETON, NEW JERSEY.
THE WILLIAM BERRYMAN SCOTT RESEARCH FUND.

PLATE I

Coccoosteus decipiens Agassiz. Section of base of denticle from infero-gnathal. $\times 85$.

PLATE II

Coccoosteus decipiens Agassiz. Section of distal portion of denticle from infero-gnathal.
 $\times 100$.

PLATE III

Stenognathus mixeri Hussakof and Bryant. Section of denticle from infero-gnathal.
 $\times 85$.

PLATE IV

Dinomylostoma buffaloensis Hussakof and Bryant. Section of symphyseal denticle from infero-gnathal. $\times 85$.

PLATE V

FIG. 1. *Coccoosteus canadensis* Woodward. Antero-supra-gnathal with postero-supra-gnathal in outer view.

FIG. 2. *Coccoosteus canadensis* Woodward. Antero-supra-gnathal with postero-supra-gnathal in inner view.

FIG. 3. *Coccoosteus canadensis* Woodward. Infero-gnathal in outer view.

FIG. 4. *Coccoosteus canadensis* Woodward. Infero-gnathal in inner view. The "blade" portion has been restored from its impression in the matrix. The originals from which all photographs on this plate were taken are in the Buffalo Museum of Science.

PLATE VI

Coccoosteus canadensis Woodward. Section of denticle from postero-supra-gnathal.
 $\times 85$.

PLATE VII

Dinichthys clarkei (Claypole). Section of denticle from infero-gnathal. $\times 85$.

PLATE VIII

FIG. 1. *Euryaspis brachycephalus* Bryant (No. 13734). Head-roof showing sutures.
 $\times 2$.

FIG. 2. *Euryaspis brachycephalus* Bryant (No. 13718). Antero-ventro-median plate.
 $\times 2$.

FIG. 3. *Euryaspis brachycephalus* Bryant (No. 13733). Head-roof showing sutures.
 $\times 2$.

FIG. 4. *Cryptaspis ellipticus* n. gen. & sp. (No. 13738). Lateral fragment of ventral shield showing sensory canals. $\times 2$.

PLATE IX

FIG. 1. *Euryaspis obscurus* n. sp. (No. 13577). Type. Head-roof showing sensory canals. $\times 2$.

- FIG. 2. *Euryaspis brachycephalus* Bryant (No. 13713a). Somewhat distorted head-roof showing part of the right sclerotic ring and domed areas over the narial sacs. The specimen is preserved in counterpart. $\times 3$.

PLATE X

- FIG. 1. *Euryaspis brachycephalus* Bryant (No. 13727). Median-dorsal plate. $\times 2$.
 FIG. 2. *Euryaspis brachycephalus* Bryant (No. 13716). Mould of visceral surface of median-dorsal plate showing overlapped areas of antero-dorso-lateral and postero-dorso-lateral. Note only faint indication of median keel. $\times 1\frac{3}{4}$.
 FIG. 3. *Euryaspis brachycephalus* Bryant (No. 13726). Uncrushed median-dorsal plate. $\times 1\frac{1}{2}$.
 FIG. 4. *Euryaspis* sp. (No. 13717). Median-dorsal plate. $\times 1\frac{1}{2}$.
 FIG. 5. *Euryaspis brachycephalus* Bryant (No. 13730). Left postero-dorso-lateral plate, showing sensory canals and areas of overlap. $\times 1\frac{1}{4}$.
 FIG. 6. *Euryaspis brachycephalus* Bryant (No. 13720). Median-ventral plate. $\times 2$.

PLATE XI

- FIG. 1. *Euryaspis brachycephalus* Bryant (No. 13709). Right antero- and postero-ventro-lateral plates, together with left antero-dorso-lateral plate; all probably from the same individual. PVL and ADL shown as impressions of outer surface. $\times 1\frac{1}{2}$.
 FIG. 2. *Euryaspis* sp. (No. 13725). Impression of left antero-lateral plate. The lower margin of this and of the following specimen is the front margin of the plate. $\times 1\frac{1}{2}$.
 FIG. 3. *Euryaspis brachycephalus* (?) Bryant (No. 13724). Mould of visceral surface of left antero-lateral plate. $\times 1\frac{1}{2}$.
 FIG. 4. *Euryaspis brachycephalus* Bryant (No. 13732). Distal extremity of spine. $\times 2\frac{3}{4}$.

PLATE XII

- FIG. 1. *Euryaspis cristatus* n. sp. (No. 13731). Type. Fragmentary median-dorsal plate showing crest with denticles. $\times 2$.
 FIG. 2. *Euryaspis cristatus* n. sp. (No. 13710). Median-dorsal plate with worn median denticles. $\times 2$.
 FIG. 3. *Euryaspis cristatus* n. sp. (No. 13729). Impression of fragmentary median-dorsal plate. $\times 2$.

PLATE XIII

- FIG. 1. *Euryaspis* sp. (No. 13714). Visceral mould of right antero-ventro-lateral plate with impression of intero-lateral plate and spine. $\times 1\frac{1}{2}$.
 FIG. 2. *Euryaspis* sp. (No. 13712). Right antero-ventro-lateral plate of a juvenile individual with intero-lateral plate and spine. $\times 2\frac{3}{4}$.
 FIG. 3. *Euryaspis* sp. (No. 13719). Visceral mould of left antero-ventro-lateral plate with impression of intero-lateral plate and spine. $\times 2$.
 FIG. 4. *Euryaspis* sp. (No. 13715). Impression of left postero-ventro-lateral plate. $\times 1\frac{3}{4}$.
 FIG. 5. *Euryaspis* sp. (No. 13723). Left antero-ventro-lateral plate with spine. $\times 1\frac{3}{4}$.
 FIG. 6. *Euryaspis* sp. (No. 13711). Impression of right postero-ventro-lateral plate of a juvenile individual. $\times 1\frac{3}{4}$.

PLATE XIV

- FIG. 1. *Anarthraspis chamberlini* Bryant (No. 13655). Fragmentary head in visceral aspect. $\times 1$.
 FIG. 2. *Anarthraspis chamberlini* Bryant (No. 13642). Left antero-dorso-lateral plate. $\times 1\frac{3}{5}$.
 FIG. 3. *Anarthraspis chamberlini* Bryant (No. 13707). Fragmentary median-dorsal plate in visceral aspect. $\times 1\frac{1}{5}$.

PLATE XV

- FIG. 1. *Anarthraspis chamberlini* Bryant (No. 13701). Head of fish lacking rostral plate and shown mostly as mould of visceral surface. $\times 1$.
 FIG. 2. *Anarthraspis chamberlini* Bryant (No. 13702). Right antero-ventro-lateral plate with antero-lateral plate and portion of spine. $\times 1$.
 FIG. 3. *Anarthraspis chamberlini* Bryant (No. 13703). Right postero-ventro-lateral (?) plate in visceral view. $\times 1$.

PLATE XVI

- FIG. 1. *Anarthraspis montanus* Bryant (No. 13704). Head of fish shown as mould of visceral surface. $\times \frac{3}{5}$.
 FIG. 2. *Anarthraspis montanus* Bryant (No. 13705). Impression of antero-median-ventral plate. $\times 1$.
 FIG. 3. *Anarthraspis montanus* Bryant (No. 13706). Median ventral plate. $\times 1\frac{1}{5}$.

PLATE XVII

- FIG. 1. *Anarthraspis montanus* Bryant (No. 13698). Left antero-ventro-lateral plate with portions of intero-lateral plate and spine. $\times 1$.
 FIG. 2. *Anarthraspis montanus* Bryant (No. 13699). Incomplete left postero-ventro-lateral plate. $\times 1$.

PLATE XVIII

- FIG. 1. *Machaeracanthus minor* n. sp. (No. 13664). Type. Spine. $\times 2\frac{3}{5}$.
 FIG. 2. *Pinnacanthus inequistriatus* n. gen. & sp. (No. 13665). Type. Spine. $\times 2$.
 FIG. 3. *Onchus peracutus* n. sp. (No. 13666). Type. Spine. $\times 2$.
 FIG. 4. *Bulbocanthus rugosus* Bryant (No. 13667). Spine. $\times 3$.

PLATE XIX

- FIG. 1. *Helenacanthus incurvus* n. gen. & sp. (No. 13662). Type. Spines. $\times 2$.
 FIG. 2. *Anarthraspis chamberlini* Bryant (?) (No. 13663). Median-dorsal plate. $\times 1$.

PLATE XX

- Gen. and spec. indet. (No. 13660). Shagreen from trunk of fish. $\times 2$.

PLATE XXI

- Gen. and spec. indet. (No. 13661). Scaled fish. $\times 1$.

PLATE XXII

Protaspis bucheri Bryant (No. 13741). Crushed fish in ventral aspect with scaled trunk. $\times \frac{3}{4}$.

PLATE XXIII

Protaspis dorfi Bryant (No. 13744). Fish in dorsal aspect showing portion of tail. $\times \frac{3}{5}$.

PLATE XXIV

- FIG. 1. *Protaspis dorfi* Bryant (No. 13744). Proximal portion of tail. $\times 1$.
FIG. 2. *Anarthraspis montanus* n. sp. (No. 13656). Fragment of bone showing denticles. $\times 2$.
FIG. 3. *Anarthraspis chamberlini* Bryant (?) (No. 13659). Detached rostral plate showing areas of overlap. $\times 1\frac{3}{5}$.

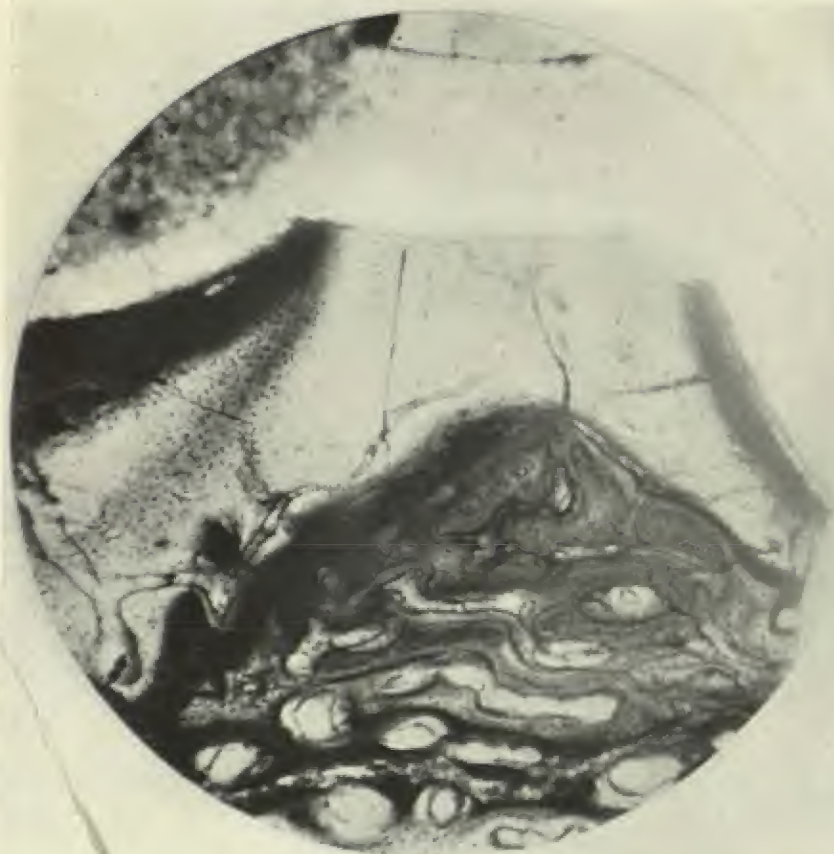
PLATE XXV

Cyrtaspis papillatus Bryant (No. 13742). Dorsal shield. $\times 1$.

PLATE XXVI

- FIG. 1. *Cryptaspis ellipticus* n. sp. (No. 13752). Type. Dorsal shield with portion of right branchial plate. $\times 1$.
FIG. 2. *Protaspis bucheri* Bryant (No. 13657). Fragment of dorsal shield showing right orbit. $\times 1$.

PLATE I



Coccosteus decipiens Agassiz. Section of base of denticle from infero-gnathal. $\times 85$.

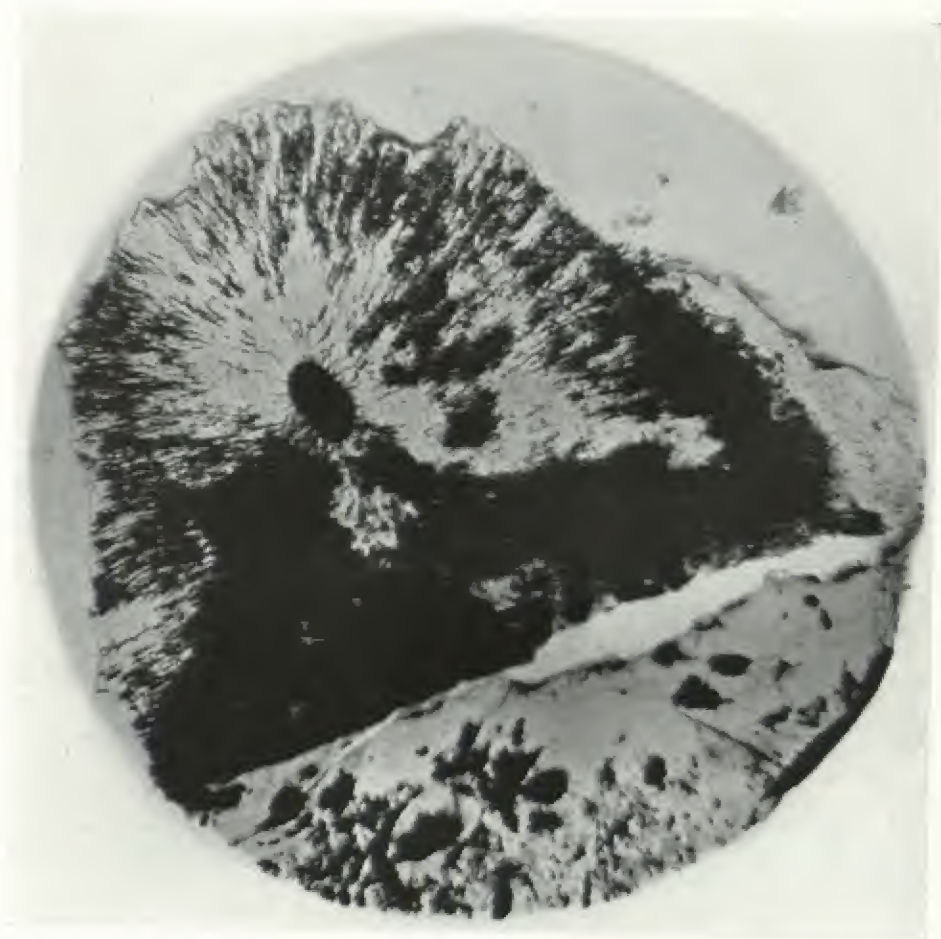


PLATE II



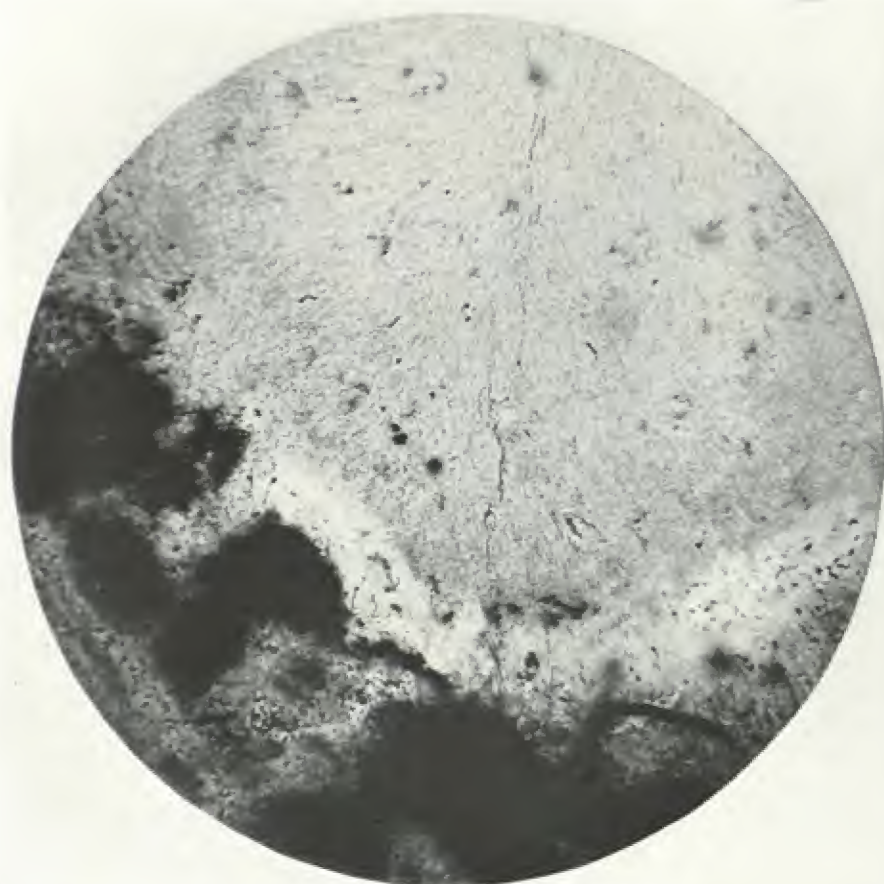
Coenosteus decipiens Agassiz. Section of distal portion of denticle from infero-gnathal.
X 100.

PLATE III



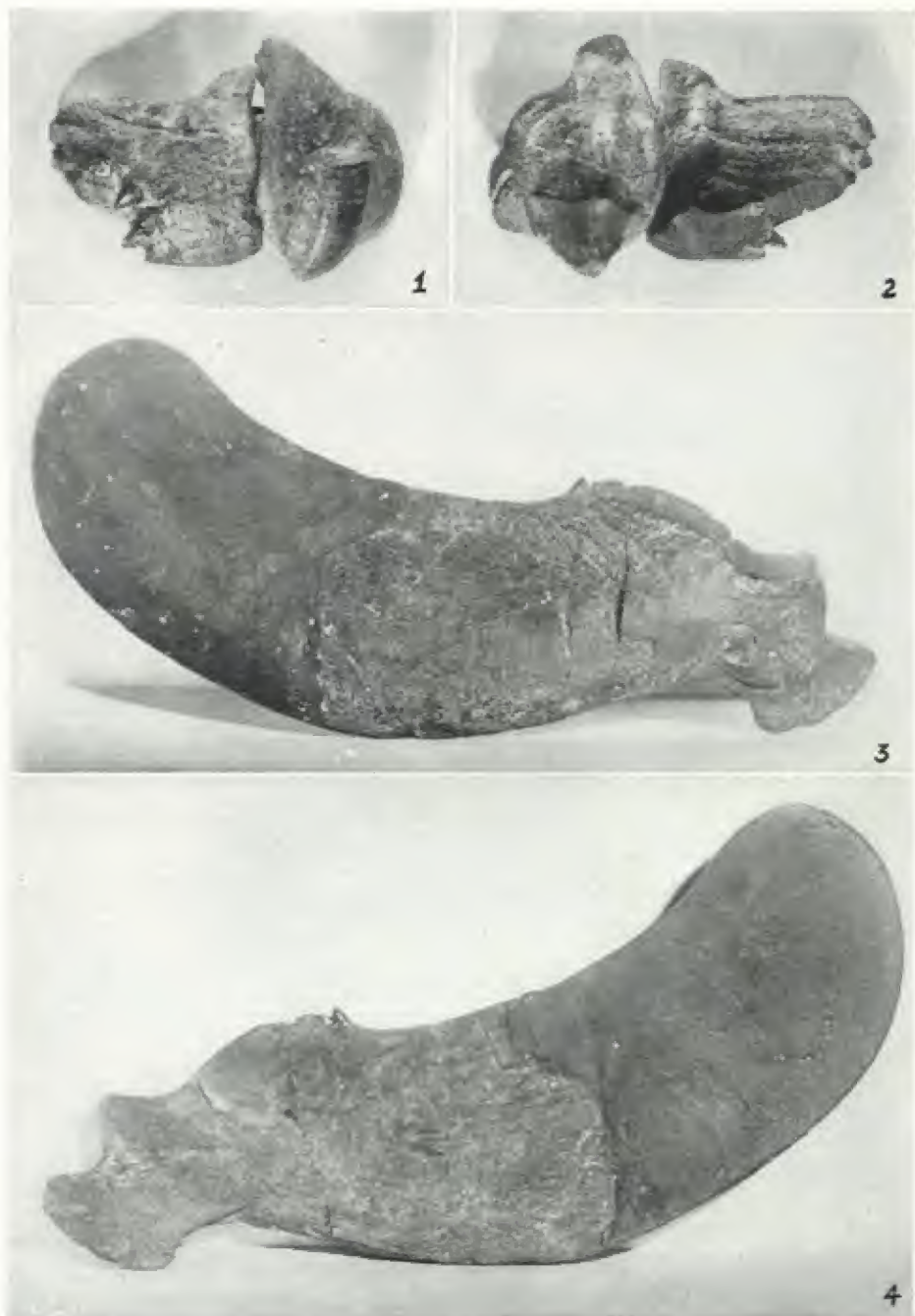
Senognathus mixeri Hussakof and Bryant. Section of denticle from infero-gnathal.
 $\times 85$.

PLATE IV



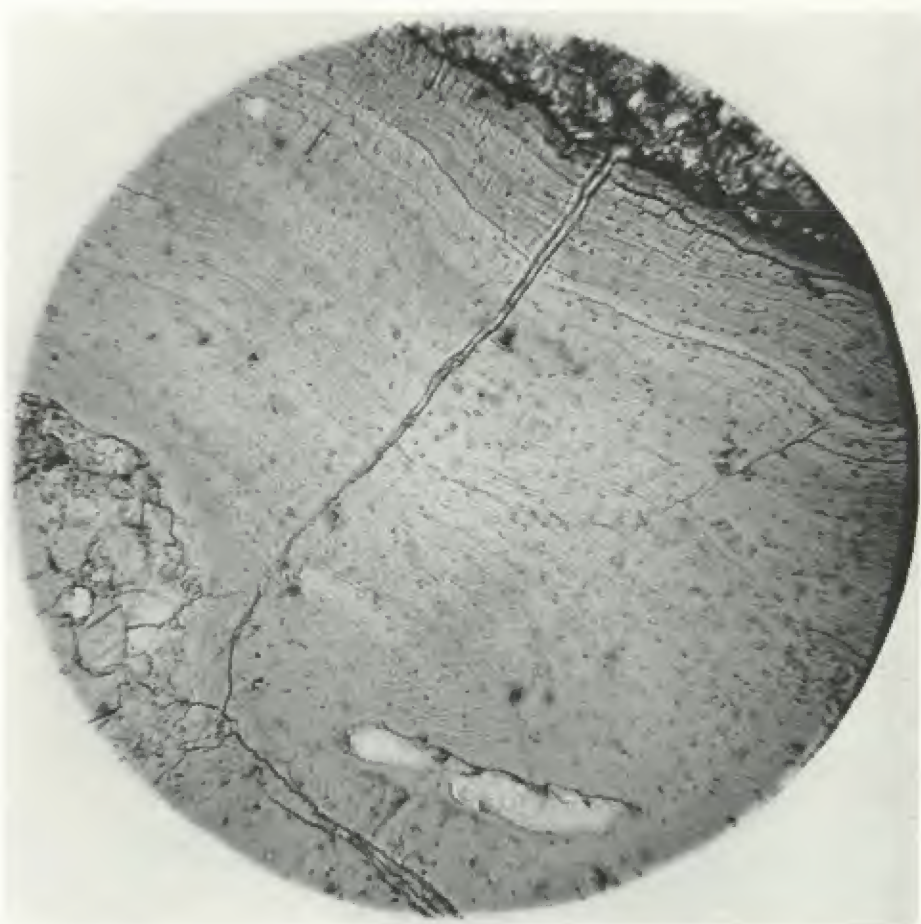
Dinomylostoma buffaloensis Hussakof and Bryant. Section of symphyseal denticle from infero-gnathal. $\times 85$.

PLATE V



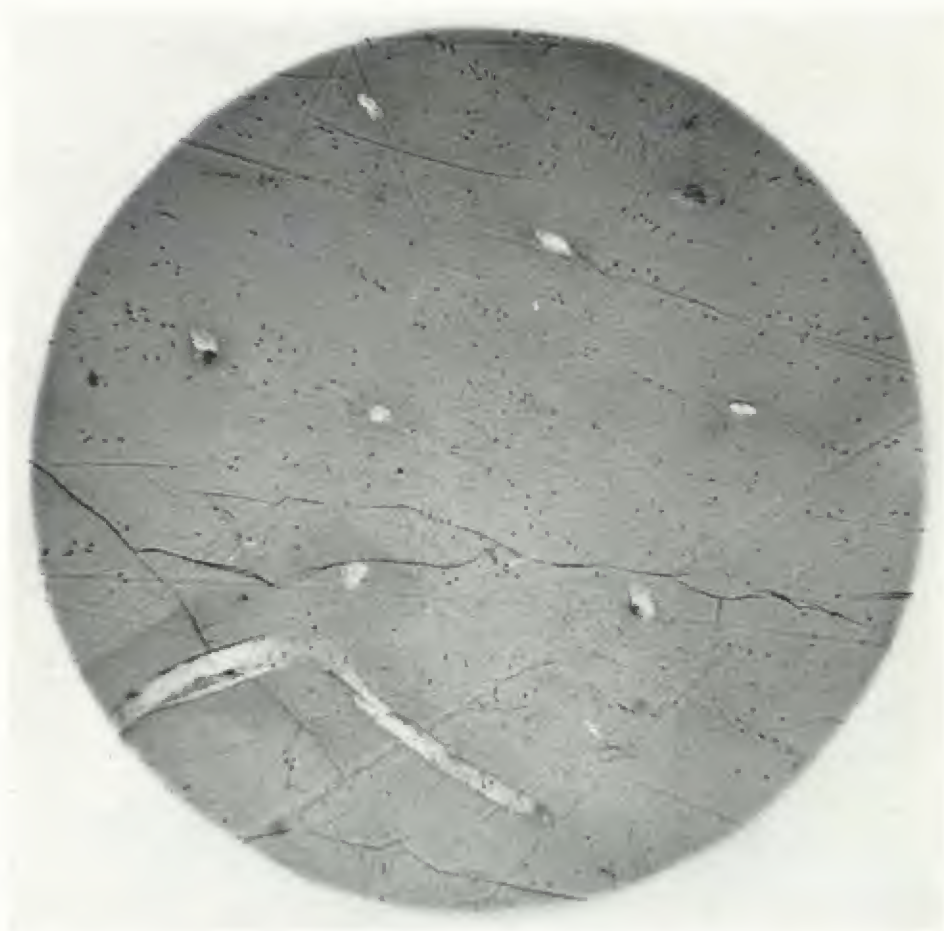
Coccosteus canadensis Woodward. For details of the 4 figures, see p. 159.

PLATE VI



Coccosteus canadensis Woodward. Section of denticle from postero-supra-gnathal.
× 85.

PLATE VII



Dinichthys clarki (Claypole). Section of denticle from infero-gnathal. $\times 85$.

PLATE VIII

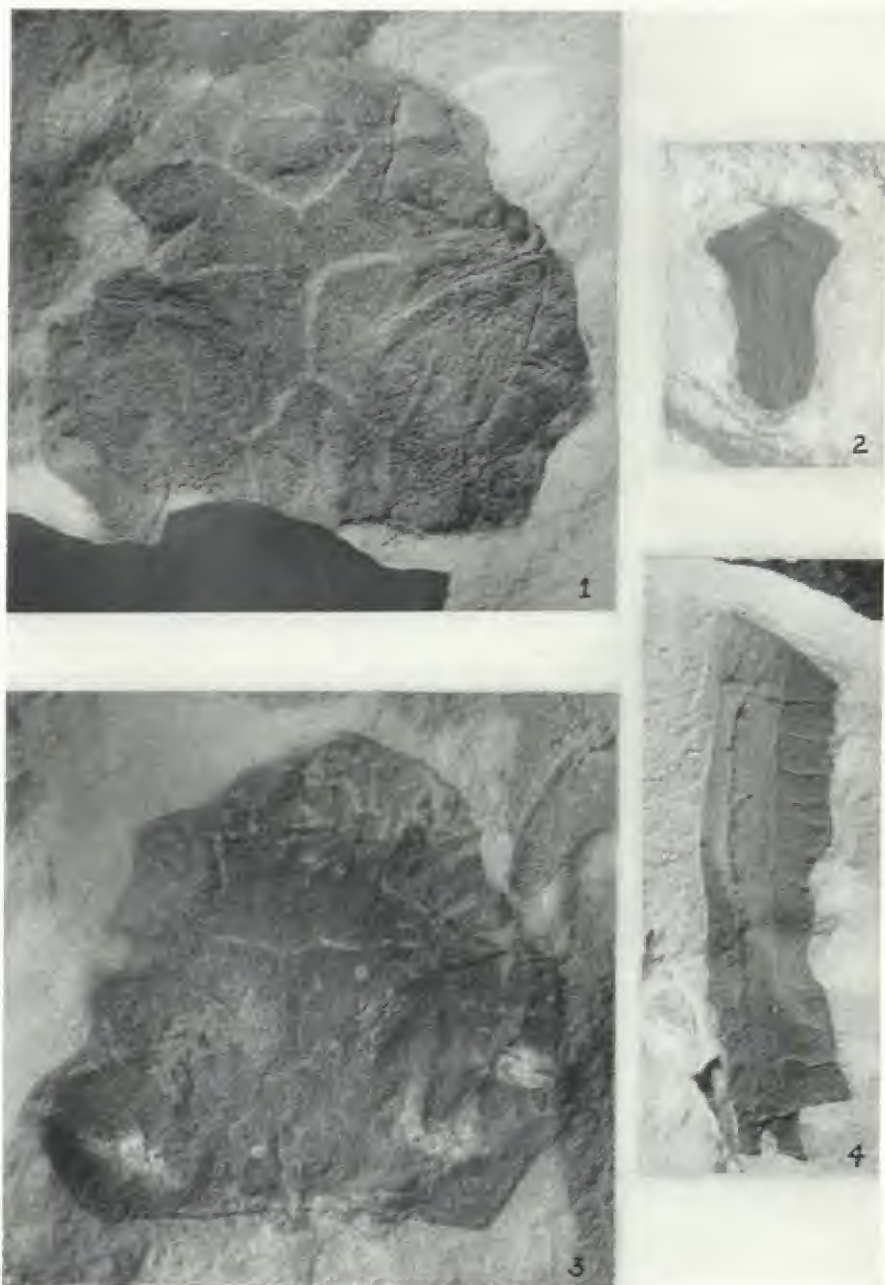


FIG. 1. *Euryaspis brachycephalus* Bryant (No. 13734). FIG. 2. *Euryaspis brachycephalus* Bryant (No. 13718). FIG. 3. *Euryaspis brachycephalus* Bryant (No. 13733). FIG. 4. *Cryptaspis ellipticus* n. gen. & sp. (No. 13738). See p. 159.

PLATE IX



FIG. 1. *Euryaspis obscurus* n. sp. (No. 13577). FIG. 2. *Euryaspis brachycephalus* Bryant (No. 13713a). See pp. 159, 160.

PLATE X

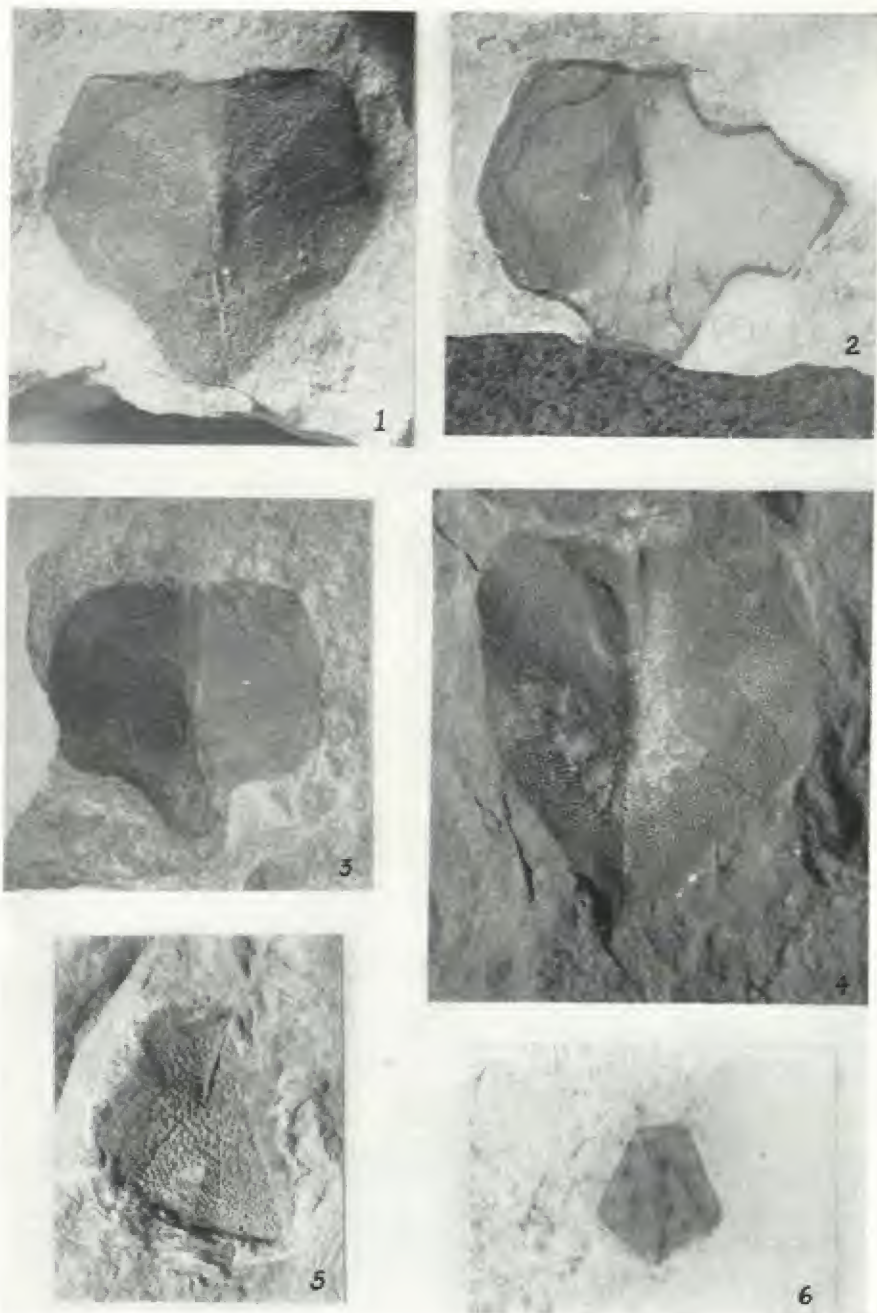


FIG. 1. *Euryaspis brachycephalus* Bryant (No. 13727). FIG. 2. *Euryaspis brachycephalus* Bryant (No. 13716). FIG. 3. *Euryaspis brachycephalus* Bryant (No. 13726). FIG. 4. *Euryaspis* sp. (No. 13717). FIG. 5. *Euryaspis brachycephalus* Bryant (No. 13730). FIG. 6. *Euryaspis brachycephalus* Bryant (No. 13720). See p. 160.

PLATE XI

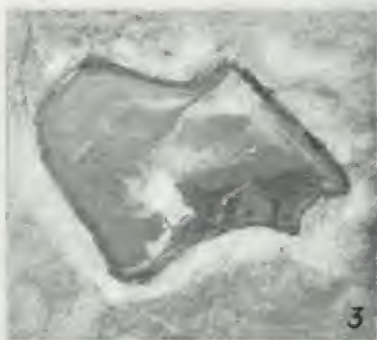
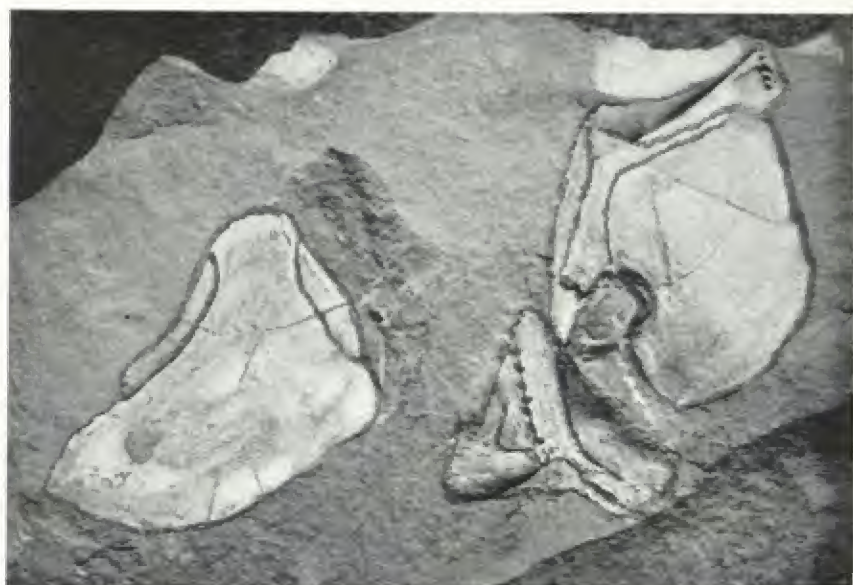


FIG. 1. *Euryaspis brachycephalus* Bryant (No. 13709). FIG. 2. *Euryaspis* sp. (No. 13725). FIG. 3. *Euryaspis brachycephalus* (?) Bryant (No. 13724). FIG. 4. *Euryaspis brachycephalus* Bryant (No. 13732). See p. 160.

PLATE XII

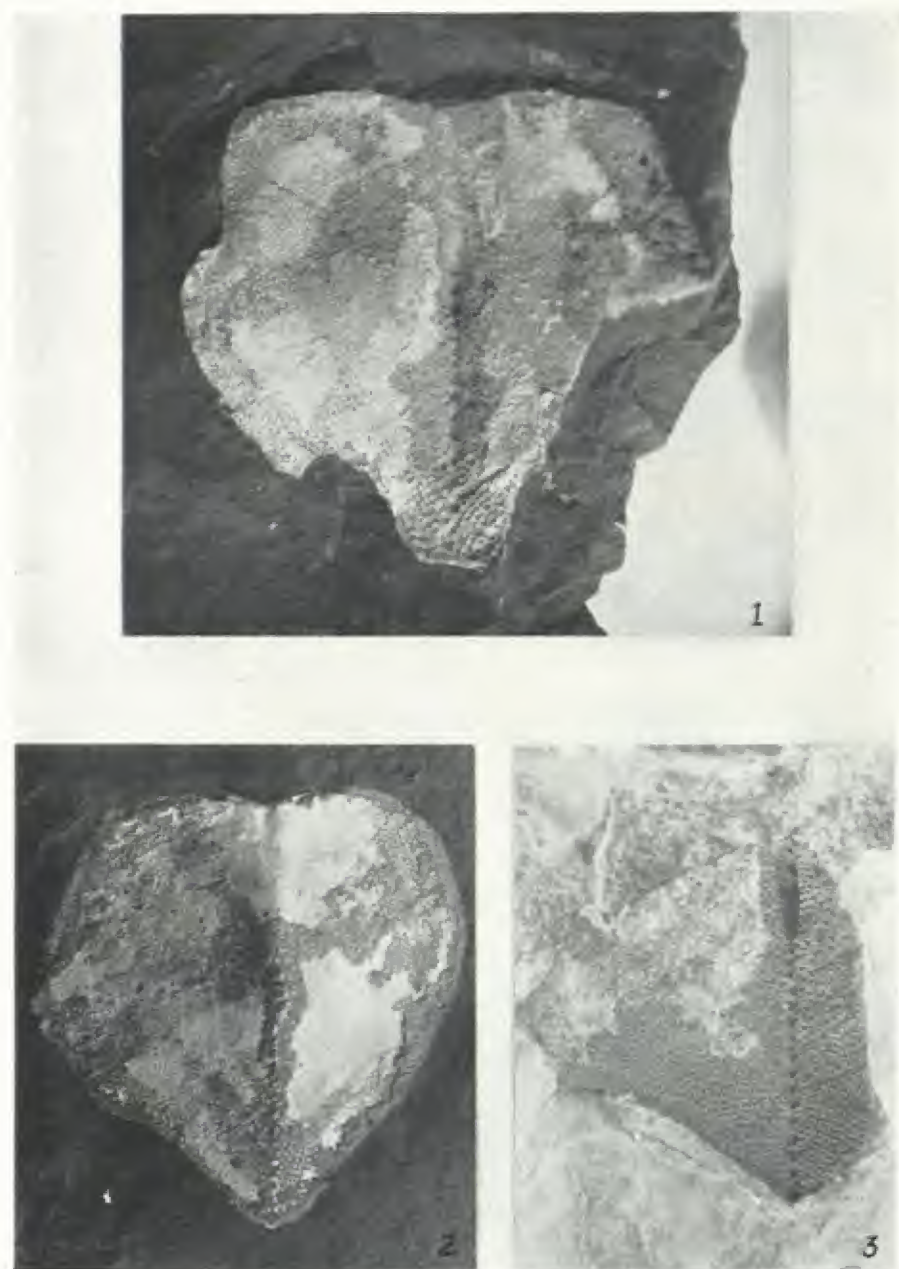


FIG. 1. *Euryaspis cristatus* n. sp. (No. 13731). FIG. 2. *Euryaspis cristatus* n. sp. (No. 13710). FIG. 3. *Euryaspis cristatus* n. sp. (No. 13729). See p. 160.

PLATE XIII



FIG. 1. *Euryaspis* sp. (No. 13714). FIG. 2. *Euryaspis* sp. (No. 13712). FIG. 3. *Euryaspis* sp. (No. 13719). FIG. 4. *Euryaspis* sp. (No. 13715). FIG. 5. *Euryaspis* sp. (No. 13723). FIG. 6. *Euryaspis* sp. (No. 13711). See p. 160.

PLATE XIV



FIG. 1. *Anarthraspis chamberlini* Bryant (No. 13655). FIG. 2. *Anarthraspis chamberlini* Bryant (No. 13642). FIG. 3. *Anarthraspis chamberlini* Bryant (No. 13707). See p. 161.

PLATE XV



FIG. 1. *Anarthraspis chamberlini* Bryant (No. 13701). FIG. 2. *Anarthraspis chamberlini* Bryant (No. 13702). FIG. 3. *Anarthraspis chamberlini* Bryant (No. 13703). See p. 161.

PLATE XVII



FIG. 1. *Anarthraspis montanus* Bryant (No. 13698). FIG. 2. *Anarthraspis montanus* Bryant (No. 13699). See p. 161.

PLATE XVIII



- FIG. 1. *Machuacanthus minor* n. sp. (No. 13664). Type. Spine. $\times 2\frac{3}{5}$.
 FIG. 2. *Piunacanthus inequistriatus* n. gen. & sp. (No. 13665). Type. Spine. $\times 2$.
 FIG. 3. *Onchus peracutus* n. sp. (No. 13666). Type. Spine. $\times 2$.
 FIG. 4. *Bulboacanthus rugosus* Bryant (No. 13667). Spine. $\times 3$.



PLATE XIX



FIG. 1. *Helenacanthus incurvus* n. gen. & sp. (No. 13662). Type. Spines. $\times 2$.
 FIG. 2. *Anarthraspis chamberlini* Bryant (?) (No. 13663). Median-dorsal plate. $\times 1$.

PLATE XX



Gen. and spec. indet. (No. 13660). Shagreen from trunk of fish. $\times 2$.



PLATE XXI



Gen. and spec. indet. (No. 13661). Scaled fish. $\times 1$.



PLATE XXII



Protaspis bucheri Bryant (No. 13741). Crushed fish in ventral aspect with scaled trunk. $\times \frac{3}{4}$.



PLATE XXIII



Protaspis dorfi Bryant (No. 13744). Fish in dorsal aspect showing portion of tail.
 $\times 3\frac{1}{2}$.

PLATE XXIV



- FIG. 1. *Protaspis dorgi* Bryant (No. 13744). Proximal portion of tail. $\times 1$.
 FIG. 2. *Anarthraspis montanus* n. sp. (No. 13656). Fragment of bone showing denticles. $\times 2$.
 FIG. 3. *Anarthraspis chamberlini* Bryant (?) (No. 13659). Detached rostral plate showing areas of overlap. $\times 1\frac{3}{5}$.

PLATE XXV



Cyrtospir papillatus Bryant (No. 13742). Dorsal shield. $\times 1$.



PLATE XXVI

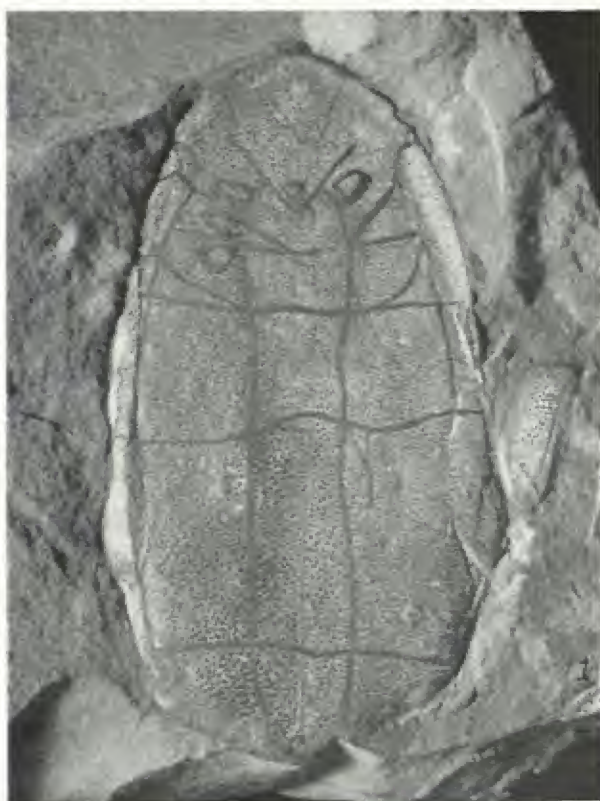


FIG. 1. *Cryptaspis ellipticus* n. sp. (No. 13752). FIG. 2. *Protaspis bucheri* Bryant (No. 13657). See p. 162.



APPENDIX

EURYPTERIDS FROM THE LOWER DEVONIAN OF BEARTOOTH BUTTE, WYOMING

BY RUDOLPH RUEDEMANN

The eurypterid material from the Lower Devonian of Beartooth Butte, Wyoming, found in association with plant and fish remains, consists of an incomplete ventral side of cephalothorax and abdomen, a posterior margin of a telson with counterpart and a fragmentary coxal joint of a swimming leg.

These jointly indicate the presence in the beds of a *Pterygotus* of fairly large size, for which the name *Pterygotus princetonii* is here proposed. In case it should be found, with more material, that the body and telson belong to different forms, the outline of the body and the characteristic swimming leg will serve to define the species.

Pterygotus princetonii sp. nov.

Type: No. 13743 Princeton University Geological Museum. Plates I-III; Text Figs. 1, 2.

Description of body. (Figs. 1 and 2.) This specimen is clearly distorted by contraction in antero-posterior direction, whereby the carapace is shorter than originally and appears relatively wide. The wrinkles along the frontal margin and the forward position of the swimming leg clearly indicate this contraction. Likewise the abdomen is much shortened and the sternites have been shoved forward below the preceding ones. The abdomen also appears thereby too broad and short, suggesting in outline that of *Eusarcus*. When, however, the segments are drawn adjoining or but slightly overlapping, the abdomen assumes a more normal elongate form.

With these corrections in mind, the body can be restored with a fair degree of approximate correctness, as shown in the outline restoration of the ventral side in Text Fig. 2. From the original specimen and this restoration the following description can be derived.

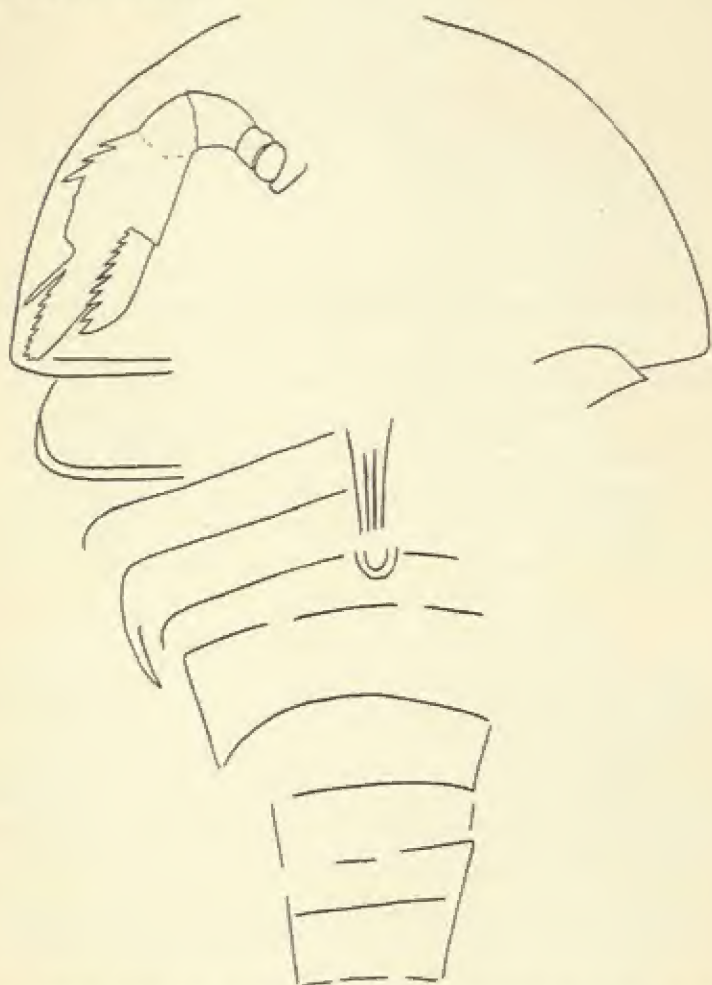


FIG. 1. Sketch of the type specimen to show certain features obscured in the photograph. \times about $\frac{3}{5}$.

Body compact, broadly obovate, about $2\frac{1}{2}$ times as long as wide, contracting somewhat abruptly to the postabdomen.

Cephalothorax. The carapace is semi-elliptic, approaching a semi-circular outline, the length originally having been undoubtedly more than half the width. The posterior margin was nearly straight transverse to slightly concave. The sur-

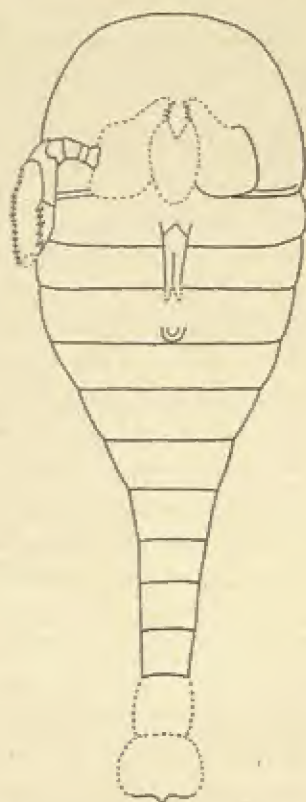


FIG. 2. Restoration of *Pterygotus princestonii*, only approximately correct. $\times \frac{1}{4}$.

face was probably fairly uniformly convex. As the ventral side of the cephalothorax alone is exposed, the eyes have not yet been worked out. There are no traces of marginal eyes observable, such as would be expected in a *Pterygotus*.

Abdomen. The right (left in specimen) portion of the operculum is preserved. Its length is at least a fifth of its width, its lateral margin running obliquely forward and inward. The following sternites are progressively shorter, their

length being about a sixth of the width. Of the postabdominal segments the first, third, fourth and fifth are preserved with their outlines, the first lacking the right margin. It would appear that these also contract more rapidly than is usual in *Pterygotus*, the first being twice as wide as the fifth. Their full length is probably not shown owing to contraction and overlap. The sixth postabdominal segment has not been seen. The posterior margin of a separate telson (Pl. II) indicates a broad telson plate with a deeply emarginate posterior margin, that is produced into a stout median spine. The fragment of the telson, five inches wide, indicates a specimen of much larger size (easily double) than the type specimen possesses. Its margin is closely set with knob-like scales.

Sculpture. The sculpture is preserved on the right side on the operculum and consists of flat crescent scales, such as are seen in *P. macrophthalmus* (see N. Y. State Museum Memoir 14, 2; Pl. 71, Fig. 9). Also the pore-system of the integument, described by the writer (see *ibid.* Pl. 80) from *P. buffaloensis* is clearly shown in the anterior sternites.

Appendages. Only one of the appendages of the cephalothorax, the right (left in figure) swimming leg is preserved on the type specimen. It resembles in general outline more the broad swimming leg of an *Eurypterus* than the more slender one of a *Pterygotus*. This, however, may be in correlation with the more compact form of the species here described.

The coxa of the swimming leg is not preserved in the type specimen. There has, however, been found with the material a separate coxa (Pl. III), lacking the manducatory edge. This with a width of 2.75 inches and a height of 3 inches is, like the telson, suggestive of a specimen twice the size of the type. There is not enough preserved of the plate to remove all doubt of its nature; it agrees however very well with the relatively enormous size and heavy character of the coxa of the swimming leg in the congeners and in the characteristic subrectangular form of its principal part.

The following segments of the swimming leg are all preserved, though the first three are worn and somewhat in-

distinct. The second to sixth segments agree in general outline with those of the other species of *Pterygotus*, notably *P. buffaloensis*; the second being short and ring-like; the third also ring-like or wedge-shaped; the fourth ring-like and broader than the preceding; the fifth still more broad and subquadrangular in outline; the sixth as in *P. buffaloensis* of irregularly rhomboidal form, but relatively larger. The seventh and eighth segments forming the paddle, compare well with those of *P. buffaloensis* reproduced in Mem. 14, Pl. 76. They also show the serration of the outer edges of the seventh and eighth segments, seen in *P. buffaloensis*, but here even more strongly developed than in that gigantic Silurian eurypterid. The "terminal palette" of the paddle of *Pterygotus* is not seen in our specimen, owing to the broken extremity of the paddle.

The opercular appendage is partly preserved in the type specimen. It is the ovipositor of a more or less mature female. It appears to have been hastate at the anterior end, as in the congeners and to have been composed of a principal sheath-like median appendage that ended in paired appendages. The third sternite bears on its posterior margin a semicircular low node of unknown function.

Horizon and locality. Lower Devonian of Beartooth Butte, Wyoming.

EXPLANATION OF PLATES

PLATE I

Pterygotus princetonii n. sp. (No. 13743 Princeton University Geological Museum).
Type. Found by Steven Fox and Princeton Summer School of Geology and Natural Resources, 1933. \times about $\frac{3}{8}$.

PLATE II

Posterior margin of telson of another specimen, No. 13740, natural size.

PLATE III

Coxal joint of left swimming leg, viewed from the inside, No. 13658, natural size.

PLATE I



Pterygotus princetonii n. sp. (No. 13743 Princeton University Geological Museum). Type. Found by Steven Fox and Princeton Summer School of Geology and Natural Resources, 1933. X about $\frac{3}{8}$.





Posterior margin of telson of another specimen, No. 1749, natural size.



PLATE III



Coxal joint of left swimming leg, viewed from the inside, No. 13658, natural size.

A HALF CENTURY OF TRITUBERCULY

THE COPE-OSBORN THEORY OF DENTAL EVOLUTION

WITH A REVISED SUMMARY OF MOLAR EVOLUTION FROM FISH TO MAN

WILLIAM KING GREGORY

Author of "The Origin and Evolution of the Human Dentition"

(Read Jan. 5, 1934)

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Osborn applies the Theory of Trituberculy to the Mesozoic and Tertiary Mammals.....	181
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PART I. HISTORICAL REVIEW OF TRITUBERCULY

Cope Founds and Develops the Theory of Trituberculy

In the judgment of palæontologists the theory of trituberculy has proved to be of great value in deciphering the evolutionary history of the dentition in many families of mammals, including man. This theory may be said to date from April, 1883, more than fifty years ago; at that time Professor E. D. Cope published his first brief note announcing his discovery that among the fossil mammals which he had discovered in the Eocene formations of Wyoming and New Mexico the "tritubercular type" of upper molar was the primitive form and that from it the more complex molar patterns of later mammals had been derived.



But this note was by no means the first of Cope's contributions to the general subject of dental evolution and before considering the theory of trituberculy itself it will be advisable to trace the principal steps that led up to it.

A little more than sixty-two years ago on December fifteenth, 1871, Cope read before this Society a paper entitled "The Method of Creation of Organic Forms," in which he took the first steps toward the elaboration of his theory of evolution of the various types of mammalian molar teeth.

With regard to the dentition, his leading idea (pp. 238, 241-242) at that time was that the more complex molar teeth of mammals had been derived from simple "tubercles" by two processes: first, "anteroposterior repetitive acceleration" of the simple cylindric type of the ordinary toothed cetacean; second, "lateral repetition, the result of a repetitive effort of growth force in a transverse direction," as in the inner fang of the sectorial tooth of a carnivore. "More complex teeth," he continued, ". . . merely exhibit an additional lateral repetition, and sometimes additional longitudinal ones. As is well known, the four tubercles of the human molar commence as similar separated knobs on the [primitive] dental papilla." His diagrams (7-12, p. 241) show clearly what he means by the principles of anteroposterior and transverse repetition in the dentition of different mammals (as explained on p. 242).

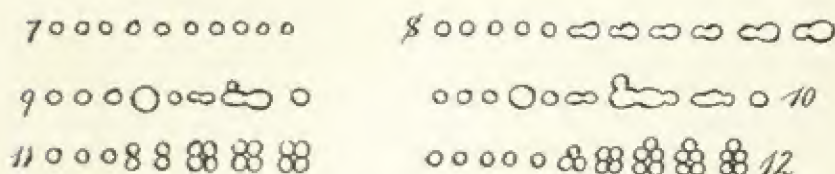


FIG. 1. The first steps. Part of Cope's diagram (1871) illustrating the principles of anteroposterior and transverse repetition in evolution. 7.—Dolphin. 8.—Squalodon. 9.—Cat. 10.—Dog. 11.—Man. 12.—Insectivore (Mole).

This was a far-reaching principle which the present writer has rediscovered and but very recently named *polyisomerism* (see p. 294). Surely there is much truth in the saying that there is "nothing new under the sun."

In 1873 Cope read a paper before the Academy of Natural Sciences of Philadelphia entitled "On the Homologies and Origin of the Types of Molar Teeth in the Mammalia Educabilia," which was published as an elaborate, well illustrated memoir in the Journal of the Academy in 1874. This contains an excellent classification of the types of molar teeth and many

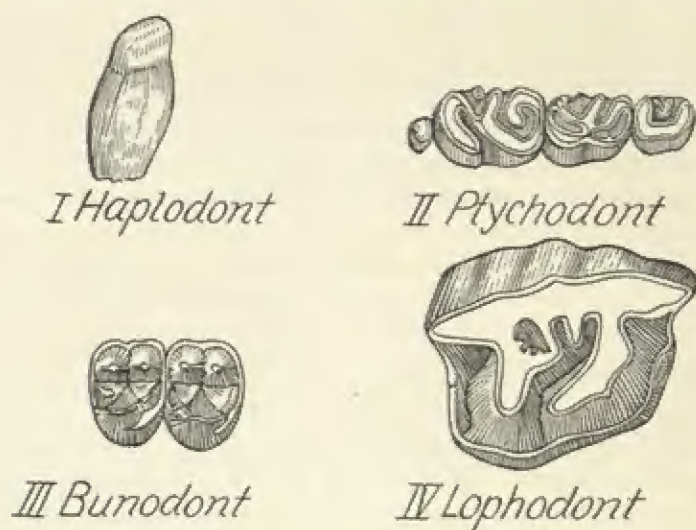


FIG. 2. Cope's four main molar types (1873).

illuminating observations on the mode of origin of the more complex molar crowns of the ungulates. His four main types, omitting subdivisions, were named and defined as follows:

Division I. *Haplodont* type: the crown undivided or simple.

Examples: the low obtuse crowns of certain dolphins, the canine teeth in general and the truncate crowns of the sloth and certain rodents.

Division II. *Ptychodont* type: the crown folded on the sides, the folds frequently crossing the crown, as in beavers, etc.

Division III. *Bunodont* type: the crown supporting tubercles, as in *Achanodon*, peccaries, raccoons, etc.

Division IV. *Lophodont* type: the summit of the crowns thrown into folds of transverse or longitudinal direction, as in ungulates.

In respect to the transverse diameters of upper and lower sets the molars of mammals are either isognathous (equal jaws), as in man, or anisognathous, in which the upper teeth overhang the lower, as in the horse.

Each of the four main divisions was subdivided into two or three sections, the details of which, for the most part, need not detain us at the present moment. It is important to note, however, that he divided the lophodonts, or more complex upper molars of ungulates, into two subordinate types (Fig. 3),

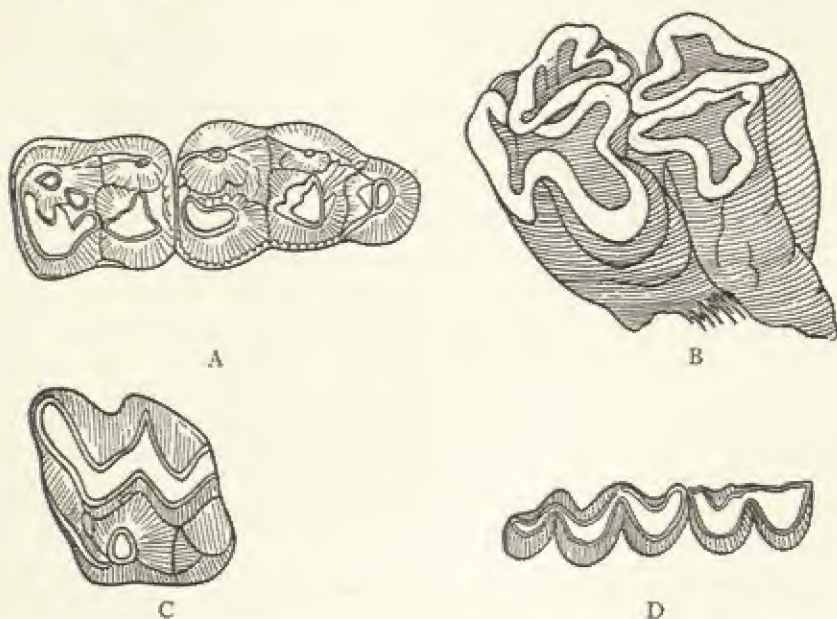


FIG. 3. Cope's Antiodont (A, B) and Amobodont (C, D) arrangement of tubercles.

A.—*Achanodon*. B.—*Hippopotamus*. C.—*Palaeosyops*. D.—*Palaeotherium*.

first, the *antiodonts*, with two pairs of crests, each representing the modification of opposite (labial and lingual) tubercles, as in ruminants such as the tapir, rhinoceros, manati, elephant;

second, the *amæbodonts*, in which the crests are derived from alternate tubercles, as in *Palæotherium*, *Palæosyops*, etc.

In his discussion of the origin of the lophodont dentition Cope observed that the four types of molars (the Haplodont, Ptychodont, Bunodont, and Lophodont) are by no means sharply defined but pass one into another by insensible gradations at many points. Then in a masterly analysis he proceeds to show how, according to his theory, each of the more complex types of lophodont molar crowns has been derived from simple bunodont types through structurally transitional stages. Thus he traces the complex lophodont upper molar of the horse back through the less complex molar pattern of *Hypohyppus* to the relatively simple type represented in "*Hipposyus*," where, as he says, "intermediate tubercles stand between the inner subconic and the exterior longitudinal crescentoid tubercles."

His concluding table (p. 85) is designed to express his view that the antiodont and amæbodont subdivisions of the lophodonts have been derived from corresponding divisions of the bunodonts. If we study this paper in the light of subsequent discovery and if we make due allowance for the fact that Cope was seeking to recognize structural sequences, not exact phylogenetic lines, we shall realize that as far back as 1873, several years before his recognition of the basic tritubercular type of molar, he had attained a generally correct idea of the broad steps in the divergent evolution of the most complex lophodont ungulate molars, starting from simple bunodont crowns with four tubercles arranged in two transverse pairs.

Cope's discoveries of various fossil remains of extinct carnivores and insectivores in the Eocene of New Mexico and Wyoming in 1872-1874 enabled him to take the next great step in his theory of the evolution of mammalian molar types.

In a remarkable article "On the Homologies of the Sectorial Tooth of Carnivora," read before the Academy of Natural Sciences of Philadelphia, February 16, 1875, Cope contributed a brilliant and, for the most part, correct analysis

of the stages of evolution of the sectorial teeth of carnivores, starting from the primitive type of lower molar illustrated in the Eocene genus *Hyopsodus* Leidy, regarded "as a modified form of quadrituberculate molar." We may paraphrase and greatly simplify his description as follows.

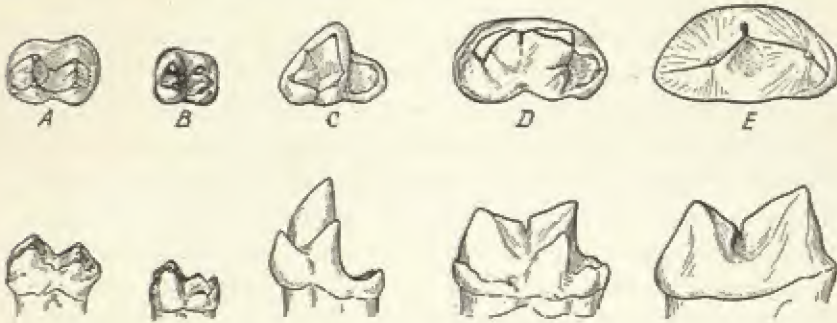


FIG. 4. Cope's theory of the origin of the lower sectorial tooth of the Carnivora. Illustrated from fossils known to Cope in 1875 and from two recent forms. Superior crown view (upper row) and medial view (lower row) of right lower molars.

- A.—*Achanodon*: showing quadrituberculate molar supposed by Cope to be primitive.
 B.—*Hyopsodus*: with oblique crest connecting posteroexternal with anterointernal tubercles. The posterior pair of main tubercles will give rise to the heel.
 C.—*Oxyena*: with derived anterointernal tubercle connected by cutting crests with anteroexternal tubercle; heel beginning to be reduced.
 D.—*Hyena*: blades of derived anterointernal and main anteroexternal tubercles greatly enlarged and directed more anteroposteriorly; primary anterointernal tubercle reduced, heel rudimentary (vestigial).
 E.—*Felis leo*: blade nearly anteroposterior in position, primary anterointernal tubercle and heel lacking.

In *Hyopsodus* the lower molar crown was somewhat compressed and bore four tubercles arranged in two pairs. In later stages the anterointernal tubercle became subdivided, while two crests grew up to connect these two cusps with the anteroexternal tubercle [now called protoconid]. Thus was formed a triangle, the basis of the cutting portion of the sectorial tooth. The anterior crest of the triangle became enlarged and blade-like, the blade gradually shifting so as to be more nearly anteroposterior in position. In the meantime the inner anterior cusp [metaconid] became reduced, while the posterior pair of tubercles formed the *heel* of the crown. In the line leading to the Sabre-teeth the heel became reduced to

a rudiment, "while in the true cats it has entirely disappeared, and the carnassial tooth remains perfected by subtraction of parts, as a blade connecting two subequal cusps."

"The development of the carnassial dentition," he continues, "has thus been accomplished, first by addition of an anterior cusp and subsequently by the subtraction of the inner and posterior cusps, so that of the original four of the quadrituberculate molar but a *single one*, i.e., the anterior external, remains." He then proceeded to show how "the Eocene forms of Carnivora frequently display more numerous sectorial teeth (such as they are) than any of the existing families." Also that the "... increased perfection of the sectorial has been associated with a reduction of other molars, first posterior, then anterior to it, which reduction has been accompanied by an increased relative size of the sectorial. By this process carnassial function has been gained and increased robustness of the jaws by progressive shortening."

Professor Cope's assistant and colleague, Dr. John A. Ryder, then took up the problem of the "Mechanical Genesis of Tooth Forms," publishing his results in the Proceedings of the Academy of Natural Sciences of Philadelphia for 1878, pp. 45-80. Starting with Cope's analysis of the mammalian tooth forms, Ryder attempted, on the whole very successfully, to correlate the different patterns of molars with corresponding movements of the mandible, basing his conclusions both on observations of the living animals in the collection of the Philadelphia Zoological Society and on examination of the relation between molar patterns and possible jaw movements in the dried skeleton. In this paper there was much of fundamental importance for the student of the mammalian dentition in action.

During the eight years from 1875 to 1883 Cope continued to pour forth a flood of reports and papers on many branches of vertebrate zoology and palæontology, including his article on the Creodonta in the Report of G. M. Wheeler . . . on the Survey West of the 100th Meridian, Vol. IV, Part 11 (1878), in which he first applied the term "tubercular sectorial" to the

lower molars of the Eocene creodonts and the modern *Didelphys*, *Centetes* and *Talpa*. For the most part, however, Cope was occupied in other fields of vertebrate zoology and palæontology and during this period wrote but little on the evolution of mammalian molar teeth.

Thus it was not until April, 1883, that he published in the *American Naturalist* his discovery that the quadrituberculate type of upper molar which he had hitherto shown to be the basic pattern for the complex upper molars of ungulates, was in its turn derived from a simpler form, the "trituberculate type." This brief communication is of so much importance in the history of odontology that it may here be reprinted in full:

Note on the Trituberculate Type of Superior Molar and the Origin of the Quadrituberculate.—It is now apparent that the type of superior molar tooth which predominated during the Puerco epoch was triangular or tritubercular; that is, with two external and one internal tubercles. Thus of forty-one species of Mammalia of which the superior molars are known, all but four have three tubercles of the crown, and of the remaining thirty-eight all are triangular excepting those of three species of *Periptychus*, which have a small supplementary lobe on each side of the median principal inner tubercle.

This fact is important as indicating the mode of development of the various types of superior molar teeth, on which we have not



FIG. 5. Transitional state between the tritubercular and the quadritubercular type of upper molar, seen in some of the *Periptychidae* (*Anisonchus sectorius*). Natural size. After Cope.

heretofore had clear light. In the first place, this type of molar exists today only in the insectivorous and carnivorous Marsupialia; in the Insectivora, and the tubercular molars of such Carnivora as possess them (excepting the plantigrades). In the Ungulates its persistence is to be found in the molars of the *Coryphodontidae* of the Wasatch, and *Dinocerata* of the Bridger Eocenes. In later epochs it is chiefly seen only in the last superior molar.

It is also evident that the quadritubercular molar is derived from the tritubercular by the addition of a lobe of the inner part of

a cingulum of the posterior base of the crown. Transitional states are seen in some of the Periptychidæ (*Anisonchus*) and in the sectorials of the Procyonidæ.

The general ideas embodied in this note were developed further in his next paper, "On the Trituberculate Type of Molar Tooth in the Mammalia," read December 7, 1883, before the American Philosophical Society. This is another brief communication but it is pregnant with significance in the light of subsequent developments. He states:

It is now apparent that the type of superior molar tooth which predominated during the Puerco epoch was triangular or tritubercular; that is, with two external and one internal tubercles. Thus, of sixty-seven species of placental mammalia of which the superior molars are known, all but four have three tubercles of the crown, and of the remaining sixty-five, all are triangular, excepting those of three species of Periptychus, and three of Conoryctes, which have a small supplementary lobe on each side of the median principal inner tubercle.

The second and third paragraphs are identical with those of his first note on the subject (see p. 176 above).

Cope then observed that the tritubercular or triangular superior molar is associated with what he had called the tubercular sectorial lower molar, which is to be seen in *Didelphys*, *Pelycodus*, etc. The mechanical action of such teeth was explained as follows.

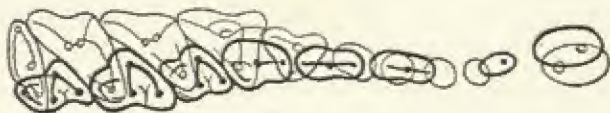


FIG. 6. Mechanical relations of the upper and lower teeth in a creodont, *Stypolophus* (= *Sinopa*) *whitii*. Natural size. After Cope, 1889.

The triangular upper molars are separated by wedge-shaped spaces with the apex external, the base opening to the palate; into this triangular space fits the triangular prism on the front part of the lower molar. The oblique edges of the inferior triangle thus shear on the edges of two adjacent upper molars. Meanwhile when the jaws are closed the heel of the

lower molar receives the impact of the internal tubercle of the upper molar. Here again, as in his earlier contributions to the subject, Cope always considered the mechanical relations of the lower to the upper teeth. He then restated his conception of the divergent evolution, on the one hand of the sectorial teeth of the Carnivora and on the other of the lophodont crowns of the Ungulata, and concluded that the "revelations of the Puerco fauna show that the superior molars of both ungulate and unguiculate mammalia have been derived from a tritubercular type; and that the inferior true molars of both have been derived from a 'tubercular sectorial' type." "Shall we look," he concludes, "for the origin of the latter [tubercular sectorial] in a tritubercular tooth also, *i.e.*, tubercular sectorial without heel; and will the crowns of the true molars of the primitive mammals alternate with instead of opposing each other? This is a probable result of future discovery."

In 1884, in an article on the Creodonta, Cope stated (pp. 258-260) that he had already pointed out that "the cone was the simple form of tooth from which all others must have been derived," and that "in the Mammalia they may have been modified in several ways simultaneously, but two methods present themselves as the most certain secondary types. The first of these is that of the simple premolar where the cone is compressed and is sooner or later followed by a horizontal extension or heel. This type persists in the inferior true molars of the Mesonychidæ. The second modification consists in the addition of lateral cusps or spines to the simple cone. Such a type is seen in inferior molars of *Spalacotherium tricuspidens* Ow. of the Jurassic period, and in some of the incisors of *Plesiadapis tricuspidens* Gerv. This form by the shifting of the two subordinate cusps to the inner side of the principal one will give a trituberculate molar of the lower series, an exaggeration of which is seen in the South African 'mole' *Chrysochloris*. If a cingulum appears at the posterior base of such a tooth we will have a rudimental 'heel,' such as is seen in *Centetes*, and is still better developed in many creodont and marsupial genera, forming the basis of the inferior

sectorial tooth of the Carnivora. This, which I have called the 'tubercular-sectorial,' is especially well marked in *Oxyæna* (Fig. 4) and *Stypolophus* (Fig. 6)."

Thus it is evident that Cope conceived of more than one way in which "secondary primitive types" of lower molars had appeared, first, by development of an incipient heel, after the compression of a premolar cone, second, by the rotation of the two small subordinate cusps to the inner side of the principal one. He was quite probably mistaken in regarding the lower molars of *Mesonyx* as primitive.

The hypothesis of the origin of the triangular lower tooth by the rotation of the two subordinate cusps to the inner side was developed by Osborn (see below, p. 181).

In April, 1885, in the course of a series of articles "On the Evolution of the Vertebrata, Progressive and Retrogressive," published in the *American Naturalist*, Cope gave a remarkably accurate outline of the evolution of the dentition.

. . . Of the two types of Monotremata, the Tachyglossidæ and the Platypodidæ, the known genera of the former possess no teeth, and the known genus of the latter possesses only a single corneous epidermic grinder in each jaw. As the Theromorphous reptiles from which these are descended have well developed teeth, their condition is evidently one of degeneration, and we can look for well toothed forms of Monotremata in the beds of the Triassic and Jurassic periods. Perhaps some such are already known from jaws and teeth. In the marsupial order we have a great range of dental structure, which almost epitomizes that of the Monodelph orders. The dentition of the carnivorous forms is creodont; of the kangaroos is perissodactyle, and that of the wombats is rodent. Other forms repeat the Insectivora. I therefore consider the placental series especially. I have already shown that the greater number of the types of this series have derived the characters of their molar teeth from the stages of the following succession. First a simple cone or reptilian crown, alternating with that of the other jaw. Second, a cone with lateral denticles. Third, the denticles to the inner side of the crown forming a three-sided prism, with tritubercular apex, which alternates with that of the opposite jaw. Fourth, development of a heel projecting from the posterior base of the lower jaw, which meets the crown of the superior, forming a tubercular-sectorial inferior molar. From this stage the carnivorous and sectorial den-

tition is derived, the tritubercular type being retained. Fifth, the development of a posterior inner cusp of the superior molar and the elevation of the heel of the inferior molar, with the loss of the anterior inner cusp. Thus the molars become quadritubercular, and opposite. This is the type of many of the Taxeopoda, including the *Quadrumania* and *Insectivora* as well as the inferior *Diplarthra*. The higher Taxeopoda (*Hyracoidea*) and *Diplarthra* add various complexities. Thus the tubercles become flattened and then concave, so as to form V's in the section produced by wearing, or they are joined by cross-folds, forming various patterns. In the Proboscidea they become multiplied so as to produce numerous cross-crests.

The dentition of some of the Sirenia is like that of some of the Ungulata, especially of the suilline group, while in others the teeth consist of cylinders. In the Cetacea the molars of the oldest (Eocene and Miocene) types are but two-rooted and compressed, having much the form of the premolars of other Mammalia. In existing forms a few have simple conical teeth, while in a considerable number teeth are entirely wanting.

After the lapse of nearly half a century that has been crowded with discoveries of new fossil mammals from many horizons, one can only wonder at Cope's amazing insight into the problem of the evolution of the dentition. All that has been done since is practically only an amplification and verification of this prophetic passage.

In 1887 in his book on the "Origin of the Fittest" Cope frequently refers to his views on the origin and evolution of the tritubercular upper and associated tuberculo-sectorial molar, but there seems to be little here that had not already appeared in his earlier papers.

In December, 1887, at the meeting of the American Association for the Advancement of Science, he traced more fully the "Mechanical Origin of the Sectorial Teeth of the Carnivora," ascribing the anterior position of the internal tubercle of the sectorial tooth to the increasing forward pressure exerted by the better-braced lower molar. After that he wrote papers on the "Mechanical Causes of the Origin of the Dentition of the Rodentia" (1888), "On the Tritubercular Molar in Human Dentition" (1888), "On the Mechanical Causes of the Development of the Hard Parts of Mammalia"

(1889) and some others, but for the most part he left to his friends Professors Osborn and Scott the further development of the theory of trituberculy.

Osborn Applies the Theory of Trituberculy to the Mesozoic and Tertiary Mammals

In 1887 Professor Henry Fairfield Osborn completed his monographic revision of the Mesozoic Mammalia of Europe and North America (1888), which he had undertaken with the view of tracing the tritubercular upper molar and the tubercular-sectorial lower molar back to their sources among the Mesozoic mammals. The minute mammalian jaws from rocks of Jurassic age in England and Wyoming had been described and figured by Owen, Marsh and others, but were evidently in need of reëxamination in the light of the theory of trituberculy. Osborn at first tentatively adopted the hypothesis put forth by Cope that the relations of reversed triangles obtaining between upper and lower molars in the

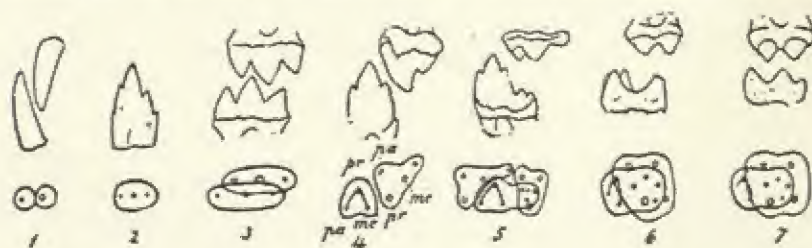


FIG. 7. Osborn's first diagram illustrating the theory of trituberculy (*Amer. Naturalist*, 1888). The legend was as follows:

"Molars of opposite jaws in normal mutual relation. 1. *Delphinus*. 2. *Dromatherium*. 3. *Triconodon*. 4. *Spalacotherium* (lower), *Peralestes* (upper). 5. *Visserratus*. 6. *Mioclanus*. 7. *Hyoprodon*."

pure tritubercular stage had been derived from the triconodont stage with three cusps in anteroposterior line by the rotation of the flanking cusps (outward in the upper, inward in the lower, molars). *Spalacotherium* of the English Jurassic showed the triangle of three simple cusps with little or no heel, and had been chosen by Cope as the first derivative from *Triconodon*, with three cusps in line, after the rotation of

the small cusps in the manner above described. The genus *Menacodon* of Marsh from the Upper Jurassic of Wyoming gave some color to this idea since the three main cusps of its lower molar had every appearance of being homologous with those of *Triconodon* and yet were already disposed in a very widely open triangle as if preceding the more acute triangle of *Spalacotherium*.

Up to this time the names usually applied to the main cusps of the tritubercular crown and its derivatives had been based on their positions with reference to certain planes and axes that were outside the tooth itself. For example, according to one system in use at that time, the four main cusps of the human first upper molar were designated as follows:

anteroexternal	posteroexternal
anterointernal	posterointernal

Professor Osborn conceived the ingenious idea of naming these cusps with reference to their origin and relations to the primary tip of the crown, so that the main cusps of a quadrutuberculate molar received the following names:

paracone	metacone
protocone	hypocone

The proto- and hypocones were on the inner, the para- and metacones on the outer side of the superior molar crown.

In the triangle of the lower molars, which was the reverse of the upper triangle, the main tip was on the outer side and therefore received the name protoconid, the termination *id* being applied to all lower cusps, while the terms paraconid and metaconid were invented respectively for the anterointernal and posterointernal cones of the lower triangle. The heel of the lower molar was called the talonid.

Osborn's memoir was illustrated by many carefully executed enlarged figures and restorations of the minute jaws of the Mesozoic mammals, together with comparative series of the principal types of incisors, canines, premolars and molars; these in turn yielded the material for subsequent dia-

grams illustrating the inferred stages in molar evolution from the simple reptilian cone to the tritubercular stage.

In later papers (see bibliography) Osborn applied the "tritubercular key," as he called it, to the elucidation of the cusp homologues of the most complex ungulate molars. He was thus able to show that the cumbersome nomenclatures which had been developed by European writers in describing the molar patterns of horses and rhinoceroses could be replaced by the simple and clear nomenclature of the theory of trituberculy.

In 1895 Professor Osborn published a diagram (Fig. 8), illustrating the origin and evolution of the upper and lower molar patterns of the Jurassic and early Eocene mammals, which has been copied in scores of later books and papers and which set forth some of the essential features of the theory of trituberculy as far as it was then understood. Unfortunately, however, its very clarity seems to have led many authors of textbooks, who had perhaps never seen any of the actual specimens, to dismiss the theory of trituberculy after scant allusions to the geometrical figures contained in the first row of the diagram, instead of studying the teeth themselves. Hence that part of the theory of trituberculy which traced the later stages of molar evolution came to be regarded as a speculation, along with the part dealing with the origin of the tritubercular molar. To return to the figure under consideration, we may note that despite its diagrammatic quality it was unfortunately misleading in important particulars. By widely separating adjacent upper teeth it made impossible a correct representation of the very mechanical relations of the upper and lower teeth which it claimed to represent; that is, in Figs. A-H the talonid cusps were thereby pulled far away from their natural positions, while the protocones were not shown in their correct positions as articulating with the basins of the talonids. Thus the most essential features for understanding the mechanical relations of the upper and lower teeth were distorted. Nevertheless the makers of many textbooks have followed each other like sheep in reprinting this diagram without critical comment.

It cannot be too often emphasized that the Cope-Osborn theory of trituberculy, as Osborn himself noted in 1907, included two distinct parts: first, a theory of the origin of the

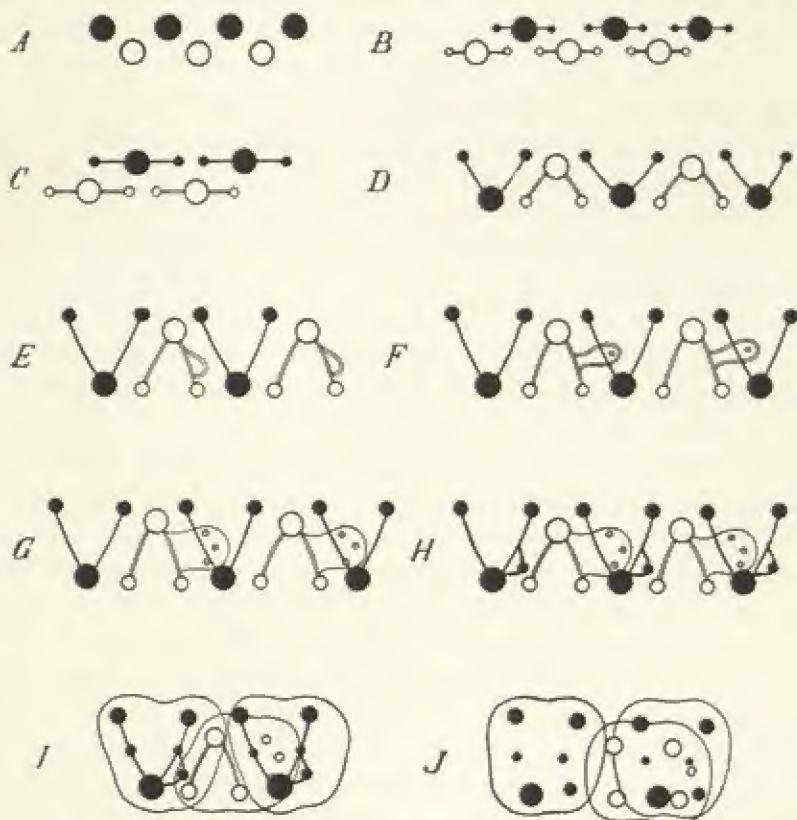


FIG. 8. Osborn's diagram of 1895 illustrating "Mechanics of Cusp Addition (diagrammatic)." The legend was as follows (1907):

"A, the conical stage; B, C, the triconodont stages; * D, the first triangular stage; † E, F, G, the triangular upper molar, the lower molars, with triangle and heel; H, I, upper and lower molars, with triangle and heel; J, human type, upper molars, with four cusps, triangle, and heel; lower molars, with five cusps, antero-internal cusp having disappeared."

* Note that the upper teeth (black) bite outside the lower teeth.

† Note that the protocones bite inside of and between the lower teeth.

tritubercular molar pattern, and second, a historical generalization to the effect that the tritubercular molar had in its turn been the origin of the more complex molar patterns of the

later mammals, especially insectivores, primates, carnivores and ungulates. The first part of the theory still lacks verification or now appears to be contradicted, at least in part, by later evidence; the second part is verifiable upon large collections of fossil teeth from successive horizons of the Eocene and later ages.

In 1907 Professor Osborn published his well known book on "The Origin and Evolution of the Mammalian Molar Teeth to and from the Tritubercular Type." With the assistance of the present writer he brought together and reprinted his numerous contributions to the subject and then gave a new illustrated review of the molar teeth in the different orders of mammals. It was shown that the multituberculates probably never passed through a tritubercular stage, that the Mesozoic trituberculates and the later marsupials, insectivores, carnivores, ungulates and primates almost certainly did pass through such a stage and that the evidence was incomplete in respect to the edentates, rodents, Cetacea, and a few other isolated groups. These chapters were followed by a critical review of opposing theories of the origin of the mammalian molar types, ending with a discussion of the evolutionary processes known as analogy, homology and homogeny, in so far as they are illustrated by the evolution of similar cusps independently in different phyletic series of mammals. Here Osborn stressed the idea of "latent homology," or pre-determination, citing the independent appearance of similarly situated cusps in the molars of related phyla—cusps that were progressively evolved after the phyla had separated from the common stock. In numerous later publications, especially the monograph on the Titanotheres (1929), he applied the term "rectigradations" to such "predeterminate" parts, including the so-called metastylids in the lower molars and the various cusps added during the molarization of the premolars. He insisted that at their first appearance such "rectigradations" were obviously too minute to be of any survival value. In more recent works, including the monograph on the Proboscidea, he has substituted the term "aristo-

genes" for "rectigradations." Tracing the slow and regular addition of conules, or "aristogenes," in the molars in certain phyla of mastodonts, he regards them as examples of creative evolution of adaptive characters originating in the "geneplasm."

From the viewpoint of the present writer, "rectigradations" and "aristogenes" are examples of polyisomerism, the budding or multiplication of larger or smaller units (p. 213). That such polyisomeres may eventually acquire an adaptive value is not disputed, but that they arose as a response to need requires further evidence.

Rival Theories

Concrescence Theory of Gaudry (1878) and the Plexodont Theory of Ameghino and Others.—In the concrescence theory of Gaudry and others, and the plexodont theory of Ameghino, it was imagined that a four-rooted molar had arisen by the concrescence of four distinct simple teeth. No real palæontological evidence in support of this theory was produced.

Unfortunately many dentists and professors of dental anatomy long ago fell into the unfortunate habit of invoking the idea of reversion for almost any irregularity or monstrosity observed in the degenerate dentition of modern *Homo sapiens*. If a molar had an adventitious root protruding on one side, that root represented to them the last stage in the absorption of a separate tooth, which in the remote and always "unknown" ancestors of man had become closely appressed to the main molars and then fused with them. It never seemed to occur to the professional odontologists to describe such occurrences as new aberrations of an extremely variable dental lamina of a decadent dentition.

The climax of the concrescence theory was reached by Gorjanovic-Kramberger in 1906, who inferred that a bicuspid arises from the concrescence of two cuspids and that one upper molar originates from four single teeth. Logically then the ancestors of man must have had not fewer than one hundred and fifty-five teeth in the adult dentition alone, a number far in excess of that of any known terrestrial mammal.

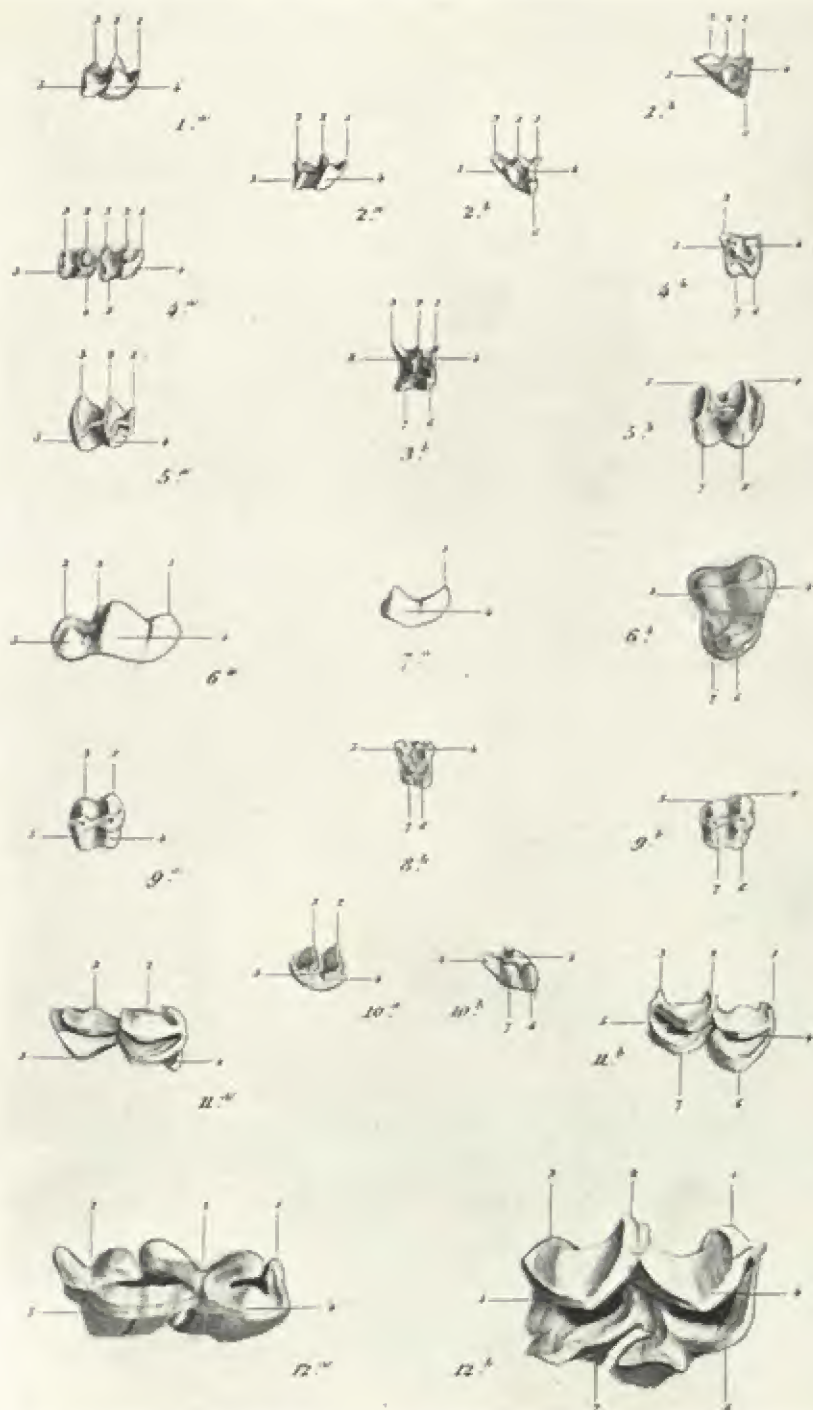
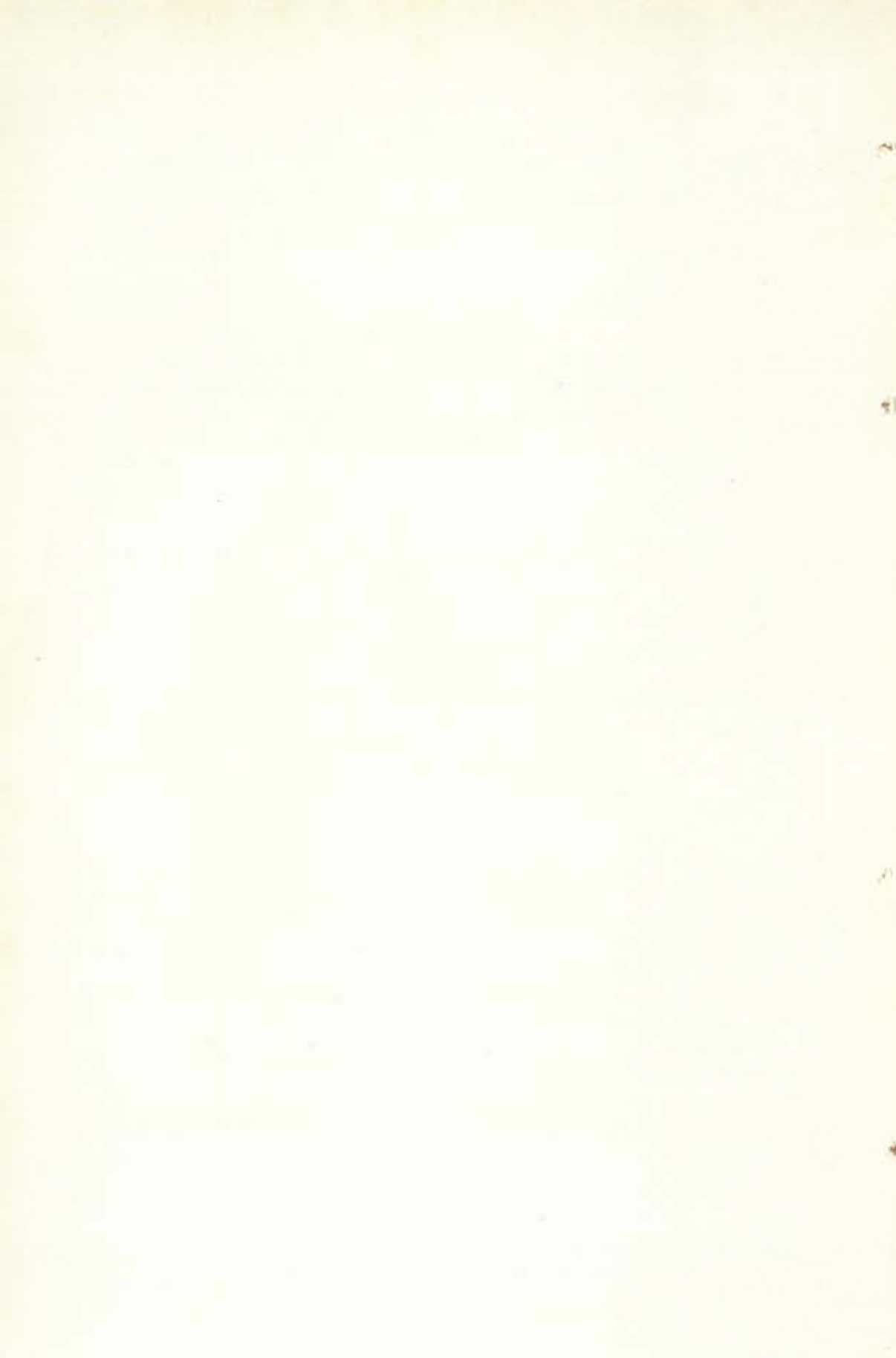


PLATE I.—Winge's Plate showing upper and lower teeth of mammals.

- | | |
|---|--|
| 1. <i>Didelphys murina</i> (?). p_3, p^4 . | 7. <i>Felis catus</i> . m_1 . |
| 2. <i>Talpa europaea</i> . m_2, m^2 . | 8. <i>Lemur</i> sp. m^1 . |
| 3. <i>Crotopus fodiens</i> . m^1 . | 9. <i>Macacus</i> sp. m_2, m^2 . |
| 4. <i>Erinaceus europaeus</i> . m_1, m_2, m^1 . | 10. <i>Mus decumanus</i> . m_2, m^2 . |
| 5. <i>Macropus</i> sp. m_2, m^2 . | 11. <i>Ovis aries</i> . m_1, m^1 . |
| 6. <i>Canis familiaris</i> . m_1, m^1 . | 12. <i>Equus caballus</i> . dp_3, dp^2 . |



Winge's Theory (1882).—Very early in the field of odontological theory, but unfortunately little known to American palæontologists because it was written in Danish, was Herluf Winge's article: "Om Pattedyrenes Tandskifte isaer med Hensyn til Taendernes Former," (On the Tooth Succession of Mammals with Special Reference to the Form of the Teeth). Inspection of his excellent plate (our Pl. 1) containing comparative views of the upper and lower deciduous teeth of recent mammals shows that he took the lower molar of *Didelphys* as the most primitive form and then homologized its W-shaped crown with the W-shaped part of the upper molar. The three points or cusps on the lingual side of the lower molar [the paraconid, metaconid and entoconid of the Osbornian system] he designated as cusps 1, 2, 3, while the two cusps on the buccal side [protoconid, hypoconid] were numbered 4 and 5. In the upper molar 1, 2, 3, were applied to the parastyle, mesostyle and metastyle on the buccal side, while 4 and 5 were applied to apices of the V-shaped paracone and metacone on the palatal side. The protocone was numbered 6 and thus had no homologue in the lower molar. Following this system, Winge consistently applied numbers to the parts of the upper and lower teeth of representative marsupials, carnivores, rodents and ungulates. The essence of his theory was evidently that the *W* of a right lower molar corresponded with the *W* of an upper molar of the same side, and that the internal projecting cone [protocone] of the upper molars was an extra element (6) preceding the addition of the hypocone (7).

From our present viewpoint Winge was correct in regarding the *W* of the lower molar of *Didelphys* as the functional antagonist of the *W* of its upper molar. He was also justified in taking the *Didelphys* upper and lower molars as an almost archetypal form from which the more specialized teeth of marsupials, carnivores, insectivores and ungulates could be derived; finally, his homologizations of the cusps in these complex patterns was from present knowledge correct, except that he mistook the enlarged protoconule and metaconule of the horse molar for the protocone (6) and hypocone (7).

In Winge's text (p. 16) he speaks of the simple conical tooth as giving rise to the tricuspid type and then refers to Owen's monograph on the fossil mammals of the Stonesfield Slate, mentioning the teeth of *Spalacotherium*, etc., as affording primitive conditions of the molars.

His biographer, Ad. S. Jensen (1924), states that Winge, in the paper under consideration, ". . . has in advance of all other authors formed a clear notion and given a record of the manner in which the more complicated forms of jaw-teeth, multicuspidate, serrate, tuberculate, plicate, may all be derived from the tricuspidate form prevalent in the elder mammals (from the Triassic and Jurassic periods) and this one again from the simple conical form belonging to the lower vertebrates."

Cope, however, has unquestionable priority in regard to the following ideas:

1871: Origin of tooth-forms by anteroposterior and transverse repetitive acceleration, starting with a single haplodont crown;

1873: Origin of lophodont from bunodont crown and of bunodont and ptychodont from haplodont type; classification of ungulate molars into antiodont and amoebodont types;

1875: Origin of the sectorial teeth of carnivores.

That the quadrituberculate and later forms of superior molars were derived from the trituberculate type was announced by Cope in 1883, on the basis of his extensive discoveries among the American Eocene Mammalia, which were manifestly unknown to Winge in 1881.

Cingulum Theories.—Among those who recognized the importance of the basal cingulum as "a mother of cusps" may be mentioned E. D. Cope, Harrison Allen (1874, see p. 197) and Marett Tims (1896). The latter, from his studies on the embryology of the lower molars of the dog, came to the conclusion that the paraconid and the metaconid were products of the basal cingulum. Recently Dr. G. G. Simpson (1929), in comparing the lower premolars of the Jurassic *Amphitherium* with its lower molars, shows that the paraconid,

metaconid and talonid were continuous below with the cingulum, especially in the posterior premolar. Hrdlička (1923) submitted the question, "What is a cingulum?" to a number of students of the human dentition but received a wide diversity of replies. It is doubtful, however, whether the structures called cingula in the human dentition are homologous with the cingula of the mammals (except those of the anthropoid apes). In many of the primitive Eocene carnivores, peripitychids, primates, insectivores, etc., the structures called cingula are sharply ridged rims on any of the four sides of the crown. They register the maximum diameters of the dental cap and there must have been a sudden shrinkage in diameter of that part of the dental cap that gives rise to the parts within the periphery. The power of the cingulum to give rise to new cusps when it occurs is not different in kind from the power of other parts of the crown to do the same thing, and in general it should be remembered that the cingulum is not a mysterious and fertile organ in itself but merely a ledge produced by an organ, which is the growing dental cap.

Embryological Theory.—It was natural that such an important and far-reaching theory, which ultimately affected the problem of the origin of man, should engage the critical attention of many investigators outside the palæontological field. In the period in which the theory of trituberculy was developed it was widely taken for granted that ontogeny repeats phylogeny, so that as soon as it had been determined, by Röse, M. F. Woodward, and others, that the so-called protocone of the molars was not the first cusp to be formed in the embryonic molars of man and other mammals, it was felt that the cardinal assumption of the theory of trituberculy, namely, that the protocone was on the inner side of the upper molar crowns, had been refuted.

Osborn's first answer to this objection (in "The History of the Cusps of the Human Molar Teeth," 1895) was virtually that there was perfect agreement between the embryological and the palæontological evidence in respect to six out of the

eight primary cusps of the upper and lower molars and that the palæontological evidence was all in favor of the protocone as being the oldest cusp; hence, he implied, there must be something wrong with the remaining embryological evidence, which was that the paracone tip was the first to become calcified.

In 1904 Osborn also replied that renewed examination of the molars of the Jurassic *Dryolestes* in the Yale Museum had demonstrated that the main high cusp of the upper molars on

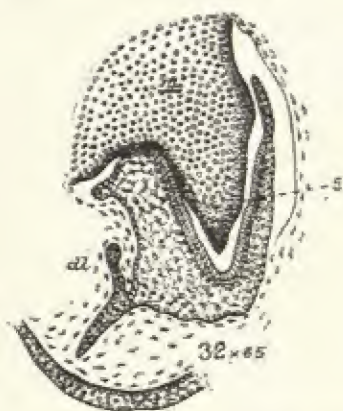


FIG. 9. M. F. Woodward's figure of the developing tooth-germ of the first upper molar of a mole, showing the protocone appearing as an internal extension from the base of the paracone.

the inner side was in line with the apex of the premolars and that it supported the other palæontological evidence that the true protocone, or original tip of the upper molars, lay on the inner side (Fig. 10). This matter will be further considered below (p. 247).

Recently a new form of the embryological theory has been put forth by Dr. M. Friant of Paris. This, however, may be more conveniently considered later (pp. 261, 266). When in the light of modern concepts of embryology one compares the figures of embryonic molars of man by Rôse (1891), of *Talpa* by M. F. Woodward, of *Equus*, *Bos* and other mammals by Friant, one is apt to be impressed by the slightness of their

resemblance to each other and by the great extent to which the embryonic molars suggest the adults of their own species. In the embryonic molar of the horse, for example, there is only a vague and very distant suggestion of the pattern of the corresponding molar of *Eohippus* but a much more direct anticipation of the molar pattern of the adult horse. Here as in other physiological processes the course of development is fundamentally anticipatory rather than reminiscent in charac-

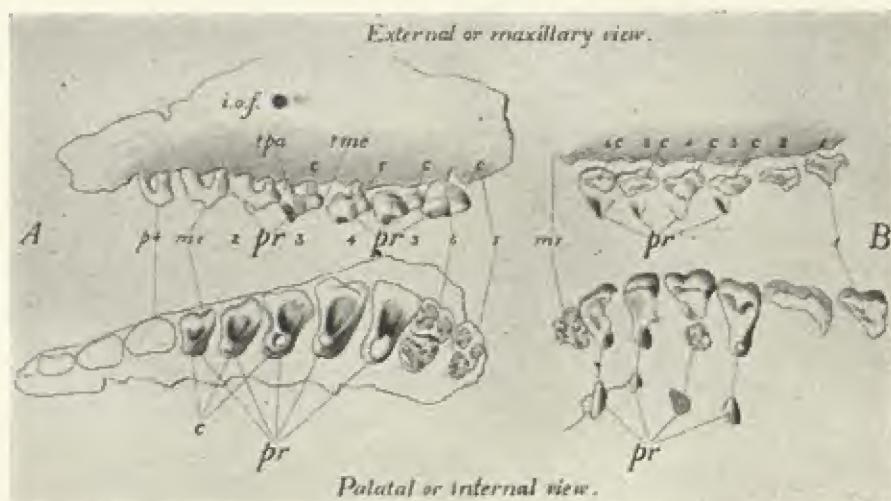


FIG. 10. Osborn's figure (1904) of the upper cheek teeth of the Jurassic "trituberculate" (pantotherian) "*Dryolestes*," indicating that the primary tip of the upper molars was on the inner or lingual side. Greatly enlarged.

ter, because the most pressing business of the embryo is to provide the ground-plan for an adult of its own species.

Polybuny Theory.—The polybuny theory, proposed by Forsyth Major in 1893, has as its main postulate the assumption that the primitive mammalian molar crown bore many cusps, not few. Its author held that the multituberculates, which are the oldest known mammals, were a stumbling-block to the theory of trituberculy. But he ignored the evidence, which has recently been very fully stated by G. G. Simpson (1928), that the multituberculates were a wholly extinct side

branch of the mammalian stem with no ancestral relationship to the typical mammals. Moreover, Forsyth Major himself traced the complex folded molars of the higher sciuromorphic rodents back to the relatively simple molar crown of *Sciurus* and he also showed how the peculiarly specialized molars of the hares and rabbits may have been derived from a type like that of *Pelycodus*, which unfortunately for his theory, is an almost orthodox trituberculate. As Forsyth Major's polybuny theory was effectively dealt with in Osborn's book on the "Evolution of the Mammalian Molar Teeth . . .," it does not seem to require additional comment at this time, except that neither the polybuny theory nor its modern variant proposed by Friant has been or could be held by North American vertebrate palæontologists or by anyone else with first-hand knowledge of the great collections bearing on the question at issue.

Bolk's Tooth-Germ Fusion Theory.—Through his remarkably thorough and comprehensive investigations of the development of the teeth in numerous reptiles and mammals of many orders, Bolk established the facts: (1) that the so-called "enamel niche" and canal in the forming tooth germ (Fig. 11 *A*) are widely distributed in the mammals and that they are made up by coalescence of distinct buccal and lingual strands of the dental lamina; (2) that the enamel septum (Fig. 11 *B*), also widely distributed among mammals, divides the enamel organ into two parts, a buccal and a lingual.

Bolk then *infers* that the enamel septum divides the future crown into two growth centres and that the fusion of the buccal and lingual strands to form the enamel niche also proves the double nature of the tooth crown, even in incisors and canines. In his composite figure or diagram (1922, p. 115, Fig. 103) he places the enamel niche directly above the enamel septum and conceives the tooth to be dimerous, consisting of a buccal protomere and a lingual deuteromere; but in other figures (1921, Figs. 59, 60, 61, 62, 63, 66) the enamel niche is definitely far to one side of the septum. He failed to explain the causal relations between the enamel niche and the enamel



FIG. 11. A. Successive cross-sections of embryonic jaw and lower medial incisors of *Macacus cynomolgus*. After Bolk.

On the lingual side of the dental cap or enamel organ is the "medial strand," which in sections *c* and *d* coalesces with the dental cap, thus enclosing the enamel niche and canal.

B. Cross-section of tooth-germ of second lower molar of *Bos taurus*, showing enamel-septum between lingual and buccal cusps.

septum and merely assumed that they were both parts of the same phenomenon, avoiding all difficulties by ceasing to discuss the enamel niche when he took up the description of the enamel septum. In his figure of the enamel septum of a developing tooth of the phalangerid *Phascolarctos* he shows that the septum is highly vascular. Here I do not see that Bolk

has proved anything beyond the possibility that the growth supplies for the forming crown sometimes at least come through this septum and are distributed on either side of it, thus forming two growth centers.

I do not understand the meaning of the enamel niche and canal unless they represent a secondary vacuity developed between the lingual and buccal borders of the dental lamina, while the strands serve to attach the tooth germ to the epithelium and to supply the material for the enamel cap. In any case these are the sole evidences that Bolk had for his immense "*petitio principii*," which was that the mammalian tooth represented a fusion or "concentration" of two successive tooth germs of a single dental family (Fig. 12). There is

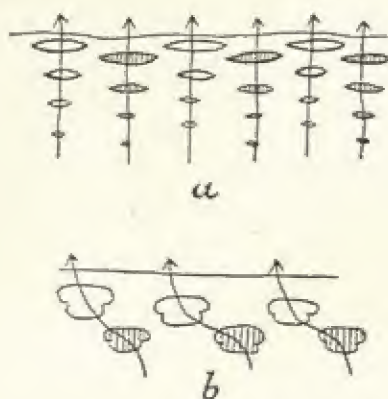


FIG. 12. Bolk's diagram (1921) showing supposed origin of mammalian tooth-germs (b) by fusion of a "dental family" of reptilian tooth-germs (a). After Bolk.

nothing, however, in his sections to prove that the parts on either side of the septum belonged to two members of a formerly vertical sequence. Moreover the enamel septum does not penetrate to the pulp cavity and in none of his numerous figures of developing tooth germs is there a suggestion that the dental pulp is made up by the coalescence of two separate pulp cavities.

Further, Bolk, like most other morphologists of the German school, took it for granted that the way in which a

tooth is formed beneath the gum is a complete and trustworthy guide to the evolutionary succession of its adult ancestors, an inference for which not a particle of direct evidence has come to my notice.

It is true that Bolk dealt with the fusion of dental germs; nevertheless he sought for evidence of such fusion in the adult teeth of modern mammals, admitting, however, that differentiation or subdivision of cusps (1922, p. 135) also contributed to the evolution of the cheek teeth of primates.

If there were anywhere in nature real evidence that a mammalian tooth has been formed by the coalescence of two or three tooth germs belonging to the same vertical series or dental family, such evidence ought to be found in the adult teeth of the mammal-like reptiles, where Bolk's protomere and deuteromere ought to be definitely indicated by the form of the crown in unworn teeth. But the crowns of the teeth in *Moschognathus* (Fig. 13) are single and undivided and the same

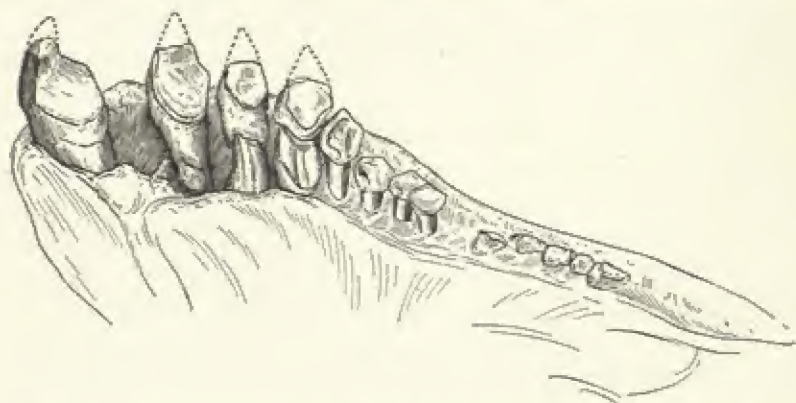


FIG. 13. Dental succession in one of the earlier mammal-like reptiles, *Moschognathus whaitsi*. From original specimen in the American Museum of Natural History. Seen obliquely from above and behind the jaw.

The two sets of teeth apparently correspond to the deciduous and permanent sets of mammals.

is true of the teeth of the young *Diademodon* described by Broom. In none of the mammal-like reptiles and in none of the numerous multituberculates, triconodonts, symmetro-

donts, pantotherians or marsupials figured in Dr. G. G. Simpson's two monographs on the Mesozoic mammals is there any objective evidence that the crowns of the incisors, canines, premolars or molars have arisen by fusion of two tooth germs.

While highly skilful both as a technician and in dialectics, Professor Bolk in dealing with the quest for the ancestral molar pattern of mammals seems to have favored a sort of Platonic idealism, as illustrated in the following sentence (1922, p. 129): "The problem resolves itself into determining the particular tooth-form in which all the potentialities possessed by the tooth-germ are completely developed and which is, as a consequence, provided with the greatest number of cusps: further, should a tooth be provided with cusps smaller in number than the greatest possible, in determining which particular potentialities of the tooth-germ are latent." Hence he conceives even the human incisor as potentially equivalent to two triconodont teeth representing respectively the protomere or buccal and the deuteromere or lingual row. The fact that not even the triconodonts themselves had triconodont incisors is ignored in all his papers. He was content to figure "triconodont" incisors in a lizard, in a dog and in primates (1922, p. 113), never sensing the impropriety of jumping from one class of vertebrates to another without examining the intervening steps.

Finally, Bolk, although boldly original in many respects, followed the wholly indefensible custom of identifying anomalies with reversions. Thus he shows (1922, p. 126) that in certain cases the tuberculum dentis of the incisors and canines of man, anthropoids and monkeys can be emphasized to such an extent as to form an almost separate tooth lying lingual to the main tooth. He at once assumes that this is a reversion to the dawn of mammalian life and identifies the lingual bud as the deuteromere derived from a reptilian replacing tooth. It is strange that anatomists and morphologists generally seem never to have dreamed that in such phenomena as double incisors and adventitious roots they were witnessing merely a phase of evolution in progress today,

a manifestation of the power of budding, which is behind the almost universal phenomenon of polyisomerism in the dentition.

The Premolar Analogy Theory.—Professor Harrison Allen may have been the originator of the premolar analogy theory. At least as far back as 1874 he taught in substance as follows:

(1) That an incisor and a canine tooth are composed respectively of one cusp and a large "cingule";

(2) That an upper bicuspid = a cuspid plus a greatly developed internal cingule, which forms the triturating surface;

(3) That a molar = a bicuspid plus an added "molar cusp" [metacone] plus a cingule [hypocone].

In the upper teeth he located the primary or "cuspid" cusp on the labial or buccal side of both the premolars and the molars. He regarded the anterointernal cusp of the molars [protocone] as an upgrown "bicuspid cusp" eventually for the cingulum.

In the lower premolars and molars he located the main or "canine" cusp on the labial side in the cusp later called the protoconid by Osborn. The inner cusps of the lower premolars were considered to be an upgrowth of the internal cingulum and to equal the inner or bicuspid cusp of the upper premolars.

The anterointernal cusp of the lower molar [metaconid] was considered equivalent to the "bicuspid" cusp of the upper molars and therefore eventually a derivative of the cingulum. The posteroexternal cusp of the lower molars [hypoconid] was homologized with the "molar" cusp [metacone] of the upper molars. Thus the entire posterior part of the lower molars was considered to be a derivative of the cuspid-bicuspid portion. The deciduous teeth were analyzed on the same principle.

Thus Harrison Allen was perhaps the first of a long series of writers to make the cardinal mistake of attempting to analyze the complex evolutionary history of the human dentition merely by inspection of modern human teeth and without

benefit of more than a minimal comparison with other mammals, recent or fossil. Such speculative theories, continued by G. V. Black and other odontologists, had a wide appeal, because they were plausible, were easily understood and were backed by some great names. They are partly responsible for the regrettably erroneous ideas of the origin of human molars that are frequently taught in dental colleges today. Thus all the treasure which has been expended in exposing the actual fossils, the only reliable basis for historical odontology, has been, so far as many dental colleges are concerned, practically wasted.

The palæontological foundations of the premolar analogy theory were laid by Professor W. B. Scott, who in his paper of 1892 on "The Evolution of the Premolar Teeth in the Mammals" showed conclusively that the premolars of the Basal and Lower Eocene mammals plainly reveal the steps by which a simple upper premolar crown became complicated toward the molar pattern (Fig. 14). First, a spur or swelling was added on its inner basal surface, later growing out into a cusp corresponding in position to the so-called protocone of the molars; second, its main high cusp became subdivided into cusps corresponding to the para- and metacones of the molars; third, the inner cusp budded off a posterointernal cusp analogous with the hypocone of the molars. However, as Scott accepted the Cope-Osborn nomenclature of the true molars, in which the original tip of the crown was identified as the protocone, or main internal cusp of the molars, and as he saw that in the premolars the original tip obviously remained on the outer side, it seemed to be necessary to apply the term 'protocone' to the main cusp of the outer side of the premolars and to invent the new terms, 'deuterocone,' 'tritocone,' 'tetartocone,' denoting the phylogenetic order of appearance of the other upper premolar cusps. Thus the strong resemblance, amounting practically to identity in appearance, which in some lines finally obtained in comparison of the crowns of the last premolar and the first true molar, was attributed to convergent evolution and the similarly situated

cusps of two adjacent upper crowns, being non-homologous, received a different set of names (Fig. 14).

In the lower premolars, however, the various phyla of Basal and Lower Eocene mammals studied by Scott showed



FIG. 14. The premolar crown patterns of mammals. After Scott, 1892.

A. Fourth upper premolar of left side, external and crown views.

1. *Deltatherium fundaminitis*; 2. *Sinopa whitia*; 3. *Cynodictis gracilis*; 4. *Felis concolor*.

Pr, protocone, d, deutocone, tr, tritocone, ps, protostyle.

B. Fourth upper and lower premolars of left side traced backward to the primitive single-tipped type.

1. *Dicotyles torquatus*; 2. *Thinohyus lentus*; 3. *Perchoerus probus*; 4. *Pantolestes brachystomus*.

that the order of cusp addition (Fig. 14) was somewhat different from that followed in the upper molars, so that corresponding differences were reflected in the nomenclature of the lower premolar cusps.

Thus the student of vertebrate palæontology found himself under the necessity of mastering two sets of names for similarly situated cusps, one applicable to the upper molars, based on the identification of the main internal cusp as the homologue of the original tip of the single-cusped crown, the other applicable to the upper premolars, based on the identi-

fication of the original tip as still lying on or near the outer or labial side of the crown. However, in the lower teeth the premolar nomenclature of Scott and the molar nomenclature of Osborn agreed in applying the name 'protoconid' to the

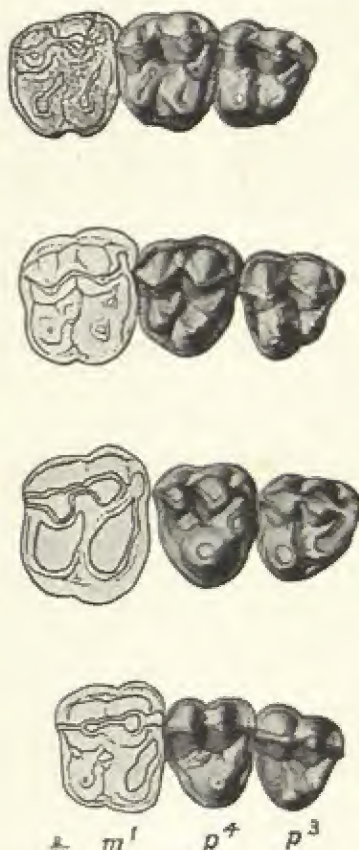


FIG. 15. Upper premolars and first molars of Eocene horses. Twice natural size. After Granger. First stage (bottom), *Eohippus borealis* (Wasatch); Second stage, *Eohippus ? venticolus* (Wind River); Third stage, *Orohippus atavus* (Lower Bridger); Fourth stage, *Orohippus progressus* (Upper Bridger).

main external cusp of the trigonid in both premolars and molars.

This curious and apparently anomalous, or at least unexplained, state of affairs excited a few critical remarks by Max

Schlosser, Fleischmann and other foreign commentators, but was long accepted as a matter of routine by field and museum workers, who were chiefly occupied with the identification of rapidly expanding collections of fossil mammals from many horizons in North America and Europe. At last, however, (1902, pp. 41-46), Dr. J. L. Wortman, formerly one of Professor Cope's field assistants and later connected with the American Museum and Yale University, in the course of his valuable studies on the fossil mammals of the Marsh Collection, sounded, so to speak, the tocsin of revolt against the, by that time, orthodox theory of trituberculy.

Two important propositions were inherent in Doctor Wortman's presentation of this theory: first, that the observed and easily confirmed history of the premolars in the Basal and Lower Eocene representatives of a certain family of creodonts (the *Mesonychidæ*) showed the steps (Fig. 16) by

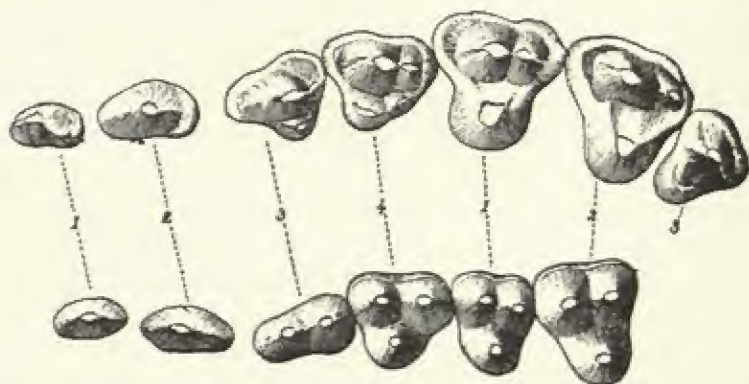


FIG. 16. Wortman's "Premolar-Analogy Theory" of the origin of the tritubercular molar from premolar stages. After Wortman.

Upper figure, *Mesonyx*; lower, *Dissacus*.

which the fourth premolar closely approached the molar pattern and made it appear highly probable that in this case the first molar was only a stage beyond the fourth premolar; in other words, he implicitly denied the necessity for adopting one set of names for the cusps of the premolars and another set for the molars, at least in the case then under consideration.

His second proposition was that in the lower cheek teeth of the oldest known Eocene sciuriform rodents the main tip of the crown had passed to the inner side in both premolars and molars, whereas in the theory of trituberculy it had been identified as the main outer cusp. From this and similar evidence he easily persuaded himself that Osborn's attempt to establish a universal system of cusp nomenclature, applicable to all sorts of mammalian molar crowns, was futile and deceptive, that the tritubercular type of molar had been evolved independently and in different ways in different groups. He therefore denied, at least by implication, all the results of Osborn in reducing the most diverse molar patterns to a single tritubercular prototype, and specifically rejected the entire nomenclature of trituberculy, returning to the earlier system of naming each cusp solely in accordance with its position in the jaw.

Dr. W. D. Matthew, however, in "The Carnivora and Insectivora of the Bridger Basin" (1909, pp. 499-502) objected to Wortman's evidence as inadequate on several grounds, including the fact that the species selected by Wortman to prove his point "do not represent the earliest and latest stages of evolution of the family and they belong to two distinct subphyla, in one of which the teeth are more nearly tritubercular than in the other"; also that on the whole the tendency in the Mesonychidæ was toward simplification of the premolars rather than the reverse. Matthew also concluded (p. 502) that two primitive types of molar seem to be indicated among the Eocene Mammalia: first, the normal and almost universal tritubercular-tuberculo-sectorial type; second, the rare zalambdodont insectivore molar, which shows a large inner and two small outer cusps on the upper molars and a high trigonid with heel rudimentary or absent in the lower molars. In the lack of known true transitional forms, each of these types may have been derived independently from the primitive reptilian cone.

From the apparent ruins of the already famous theory of trituberculy Dr. James W. Gidley of the United States

National Museum endeavored to build anew and to conserve as much as possible. In a notable paper entitled "Evidence Bearing on Tooth-cusp Development" (1906) he developed the premolar analogy theory (Fig. 17) to its logical conclusions, which were in substance as follows: (a) that the so-called protocone of the upper molars, far from being the original tip of the crown, was really an upgrowth of an internal spur from the base of the crown; (b) that it had arisen *pari passu* with the development of the talonid of the lower molars, into the basin of which it always fitted. The talonid, according to the Cope-Osborn theory, had appeared after the establishment of the trigonid. The same was true, he proclaimed, of its functional partner, the protocone of the upper tooth. The real but hitherto unrecognized heir of the original tip of the crown was, according to Gidley, the paracone. Thus, he implied, the palæontological evidence regarding the priority of the paracone over the protocone is in harmony with the evidence from embryology as to the order of calcification of the cusps.

With regard to the Cope-Osborn nomenclature of mammalian molars, Gidley recognized that it had become the common property of vertebrate palæontologists all over the world and had proved extremely convenient and useful in describing the most diversified molar patterns in nearly all orders of mammals. It is true, he argued, that the fundamental tritubercular pattern may have been evolved more than once and from different beginnings in different orders of mammals; but once it has appeared, let us retain the convenient Cope-Osborn nomenclature for its several main cusps, remembering, however, that the so-called protocone is not the oldest cusp of the crown but merely the historical datum-point for the system of nomenclature.

As noted above, the premolar analogy theory of Wortman and Gidley makes a strong appeal because it is based upon the direct evidence from successive stages in premolar evolution of many phyla of mammals, and because it apparently reconciles the otherwise conflicting evidence of embryology and

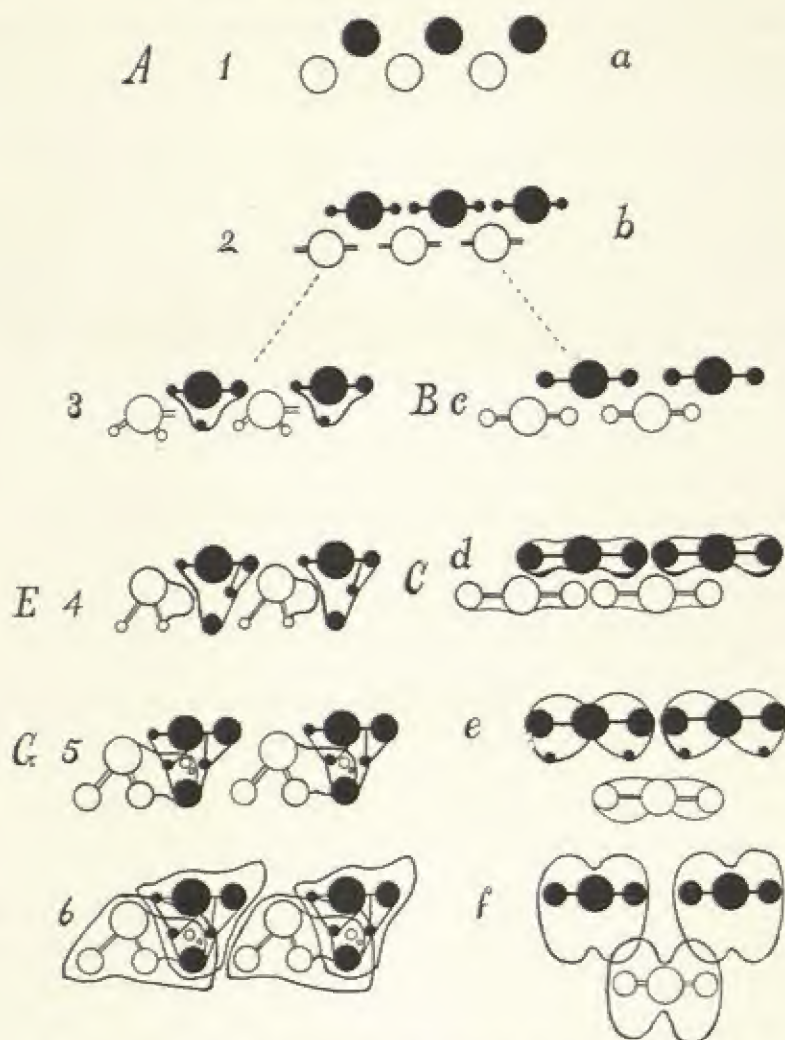


FIG. 17. Gidley's modification of the Premolar-Analogy Theory. After Gidley. Suggested Phyletic History of Two Types of Complex Molars. [As in Osborn's diagram [see Fig. 8, p. 184], the solid black dots represent the cusps of the upper molars, the circles, those of the lower molars.] 1-6, Phyletic history of the "Tritubercular" type; a to d, Phyletic history of the "Triconodont" type; e, f, From the brachyodont Triconodont stage to the bilobed hypsodont type of molar.

A, B, C, E, and G compare with A, B, C, E, and G in Osborn's diagram [see Fig. 8, p. 184]; 4, *Dryolestes* type, Atlantosaurus beds (? Upper Jurassic); 5 and 6, *Protolambda* or *Pedimys* type, Laramie beds (Upper Cretaceous); d, *Triconodon* type, Atlantosaurus beds (? Upper Jurassic); f, *Palaeolagus* type, White River beds (Oligocene).

palæontology. To these I added in 1916, 1921 and 1922 the support afforded by further studies of the occlusal relations (Fig. 18) of the upper and lower cheek teeth. It was pointed out that according to the Cope-Osborn theory of trituberculy the protocones of the upper molars fitted into the talonids of the lower molars, while the alleged protocones of the upper

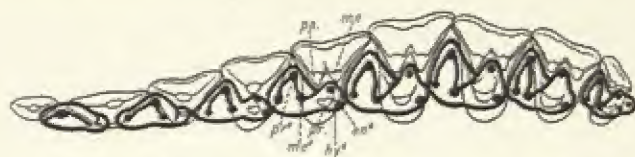


FIG. 18. Occlusal relations of the upper and lower cheek teeth illustrating supposed stages in transformation from premolar to molar patterns in a generalized mammal. After Gregory, 1916.

The crown pattern of the lower teeth is shown in heavy black lines.

This diagram does not represent any particular genus, but is based upon the conditions observed in many early Tertiary mammals. The number of teeth in the diagram is not significant or typical. The talonids of the lower molars are represented as being narrow, as they are in *Amphitherium* and other Mesozoic mammals. In most Tertiary mammals the talonids are wide.

premolars overhung the trigonids of the lower premolars; but according to the premolar analogy theory, no such apparent contradiction was involved.

It was also shown that the main tip of the premolars had the same relation to the external cingulum and to the main roots as do the para- and metacones of the molars, which according to the premolar analogy theory represent the divided tip of the molars. For these and other reasons, in the papers noted above I followed Gidley in adopting the premolar analogy theory, while retaining the Cope-Osborn nomenclature of the cusps.

More recently an important reinforcement to the premolar analogy theory was afforded by the discovery of several fossil skulls of Upper Cretaceous placental insectivores in the Cretaceous of Mongolia by Walter Granger, Chief of Staff in Roy Andrews' Central Asiatic expeditions for the American Museum of Natural History. In these precious specimens, which were described by Gregory and Simpson in 1926, the

upper molars were plainly of such a primitive tritubercular type that one of them was named *Deltatheridium pretrituberculare* (Fig. 19), especially since the para- and metacones were apparently just separating from each other. Now these

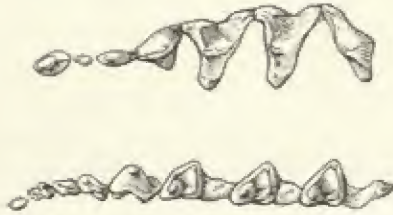


FIG. 19. Cheek teeth of Upper Cretaceous Mongolian insectivore, *Deltatheridium pretrituberculare*. $\times 3/1$.



FIG. 20. Relations of main tips of molars and premolars in a primitive Cretaceous placental (*Deltatheridium pretrituberculare*). After Gregory, 1926.

A. Oblique rear view of left lower cheek teeth, showing the protoconids of the molars in line with the tips of the premolars.

B. Oblique rear view of right upper cheek teeth, showing the high paracone in line with the tips of the premolars and the "protocone" as a low process from the base of the paracone.

para- and metacones were so exactly in line with the tips of the premolars as seen from the rear (Fig. 20) that they presented a strong appearance of being completely homologous with them. The protocones of the molars also were in series with the incipient internal swelling of the base of the fourth upper premolar and apparently homologous with it. Since these Upper Cretaceous mammals were older than the placental mammals of the Paleocene and later epochs, and since their

dentitions had many signs of relatively great primitiveness, it seemed to me at that time that they afforded practically conclusive evidence in favor of the premolar analogy theory. All the zalambdodont insectivores, from the Paleocene *Palæoryctes* of Matthew onward, strongly support the inference that the inwardly-grown paracone (or para- plus metacone) of the molars is homologous with the tip of the premolars, and that the internal basal cusp or "protocone" is homologous with the internal cingulum of the premolars (Fig. 21). Of course this resemblance between the low internal cusp of the molars and that of the premolars may conceivably be due to convergence, but as the same resemblance between the premolars and molars is found in many phyla of Paleocene and Eocene placentals, it seems arbitrary to refer it all to convergence.

Accordingly, last year when I supervised the construction of an enlarged series of models illustrating the evolution of the premolars and molars in a series of eight stages leading up to man (Fig. 70), I applied the same colors to the cusps of the premolars as to the corresponding cusps of the molars, using the Osbornian terms, however, for both the premolars and the molars. At the same time I was again assailed by doubts when I attempted to apply this system to the premolars and molars of the Jurassic pantotherians, formerly called trituberculates, which had meanwhile been intensively studied and fully described and illustrated in two splendid memoirs by Dr. G. G. Simpson. At this point, however, it seems advisable to go back to an earlier phase of my own studies on this subject.

The Wedge Theory.—In 1910, in my book on *The Orders of Mammals* I gave extended consideration to the Mesozoic mammals, in order to reconcile, if possible, the conflicting evidence of the Cope-Osborn tritubercular theory and the premolar analogy theory. While accepting the evidence cited in 1904 by Osborn to the effect that the true protocone of the Jurassic *Dryolestes* was the high internal cusp of the upper molars, I combatted that phase of the Cope-Osborn

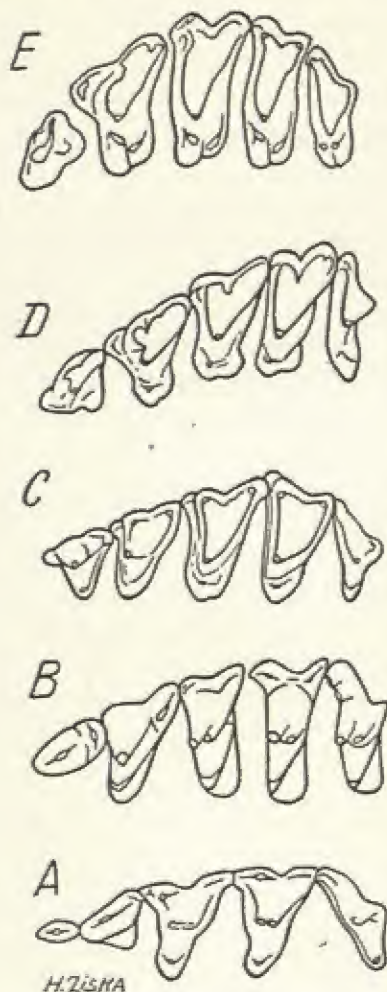


FIG. 21. Comparative drawings of left upper cheek teeth of fossil and recent zalambdodonts. From Schlaikjer, 1933.

A. Deltatheridium pretrituberculare. *B. Palaeoryctes puercensis.* *C. Apternodus gregoryi.* *D. Microgale dobsoni*, A.M.N.H. No. 31261. *E. Solenodon paradoxus*, A.M.N.H. No. 28270. (*A.* and *B.* after Simpson.) Not to scale.

theory which taught that the upper and lower molar triangles had arisen by the rotation in opposite directions of the para- and metaconids of the upper and lower molars, outward in the upper ones, inward in the lower. I concluded that, on the contrary, the evidence indicated that at a very early

period the upper molar crowns (Fig. 22) were already very unlike those of the lower molars, that they were larger and wider and that the subsequent relations of reversed triangles had been reached not through rotation of cusps but through differential growth of the crowns in such a way that the small lowers wedged into the triangular spaces between the transversely extended uppers. At that time I was unaware of the

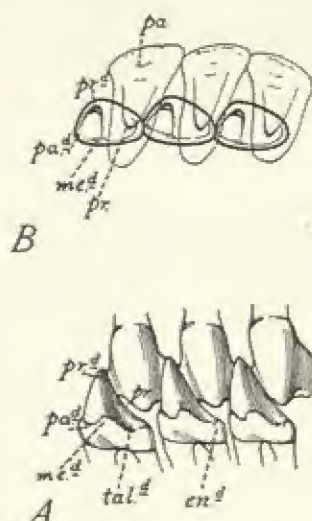


FIG. 22. Hypothetical reconstruction of the upper and lower molars in the ancestors of the Trituberculata. After Gregory, 1910.

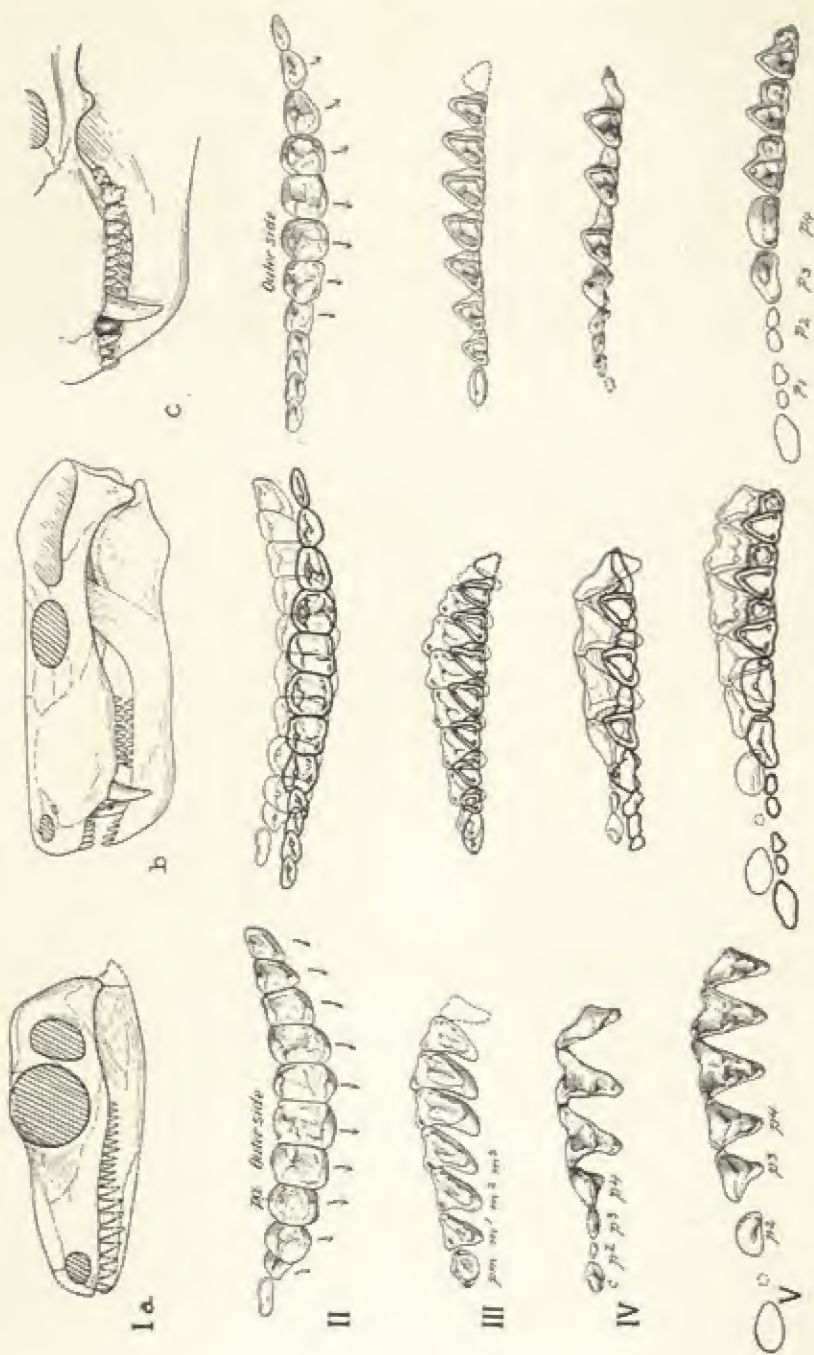
A. Internal view showing paraconid (*pa.d*), metaconid (*me.d*), entoconid (*en.d*), growing up from the internal cingulum; protoconid (*pr.d*) pyramidal, talonid (*tal.d*) receiving tip of large protocone (*pr.*) of upper molars. Right side.

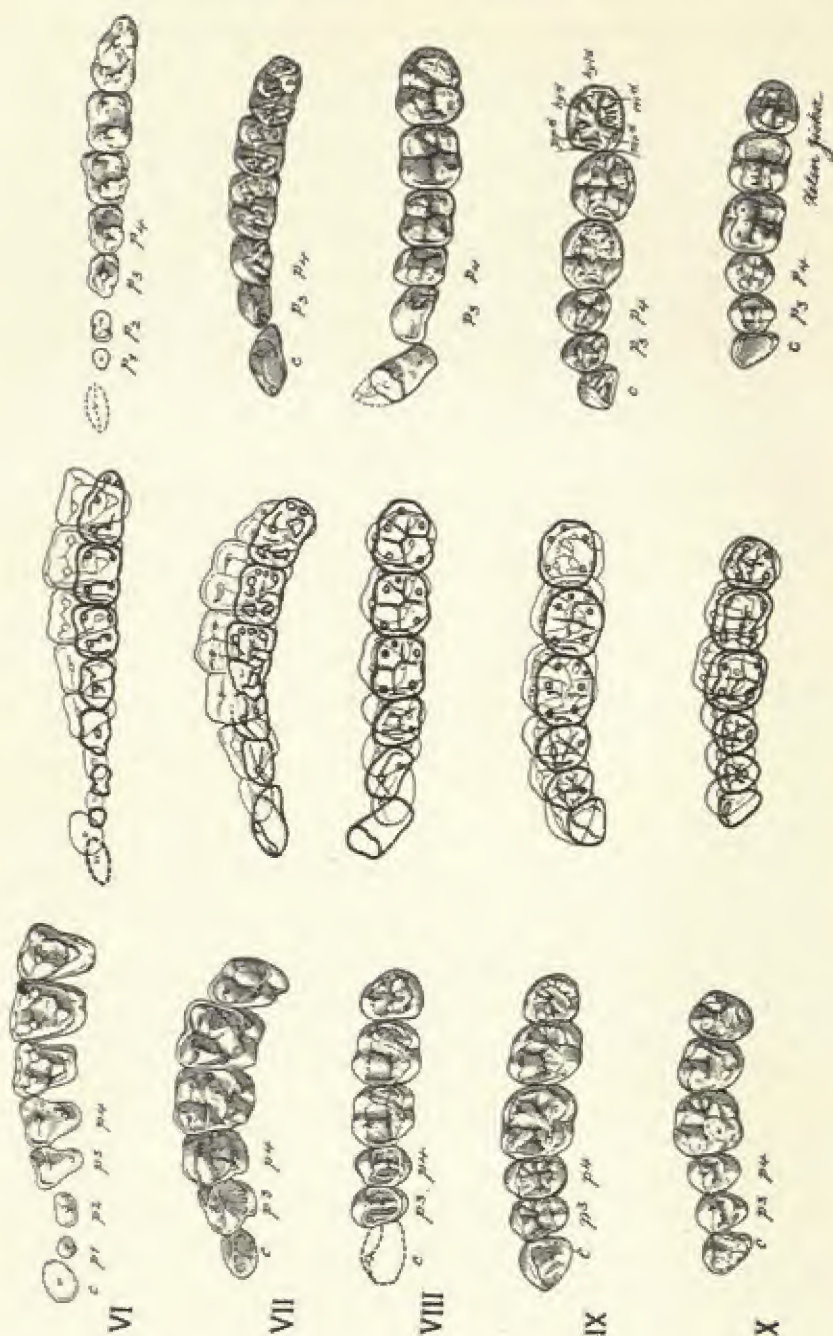
B. Projection of upper on lower molars. Protoconids and metalophids fitting between protocones; paracone (*pa*) centro-external, incipient.

[Compare the author's present views, summarized in Fig. 44 below.]

fact that the wedge-like relations of the upper and lower tritubercular molars had been observed and their significance partly appreciated by Cope as far back as 1883 (see above, p. 177).

The wedge theory I am now convinced contained a clue to the true history of the upper and lower molars during early Mesozoic times. A more developed form of the wedge theory was published by me in 1926, in which it was indicated (pp. 405, 406) that the crowns of the upper molars (Fig. 23) had





at a very early period enjoyed a rapid transverse extension, producing the conditions observed in the transversely wedge-shaped upper molars of the Jurassic "trituberculates." The further consideration of the problem of the origin of the protocone of the upper molars had better however be deferred until the final chapter, after the revised summary of molar evolution in the vertebrates as a whole.

The theory of dental evolution proposed by Dr. M. Friant in 1933 will also be considered below in the chapter on specialized mammalian dentitions.

PART II. REVISED SUMMARY OF MOLAR EVOLUTION FROM FISH TO MAN

Adaptive Radiation of Molars in Lower Vertebrates

Ostracoderms and Lampreys.—The ostracoderms are of supreme interest on account of their great antiquity and primi-

FIG. 23. Development of the wedge theory of internal extension, the author's combination of the Cope-Osborn and premolar analogy theories, illustrating the evolution of the cheek teeth from the primitive theromorph type up to the human stage. After Gregory, 1926.

- I. Substage *a*. Permo-Carboniferous. *Mycterosaurus*, primitive theromorph reptile. After Williston.
- Substage *b*. Permian. *Scylacosaurus*, primitive mammal-like reptile. After Broom.
- Substage *c*. Triassic. *Cynognathus*, advanced mammal-like reptile. After Seeley.
- II. Triassic. *Diademodon*, advanced mammal-like reptile. Mainly after Seeley. Occlusion diagram by author.
- III. Jurassic. Pantotherian (primitive pro-placental). Kindness of Dr. G. G. Simpson. Occlusion diagram by Simpson.
- IV. Cretaceous. Pre-trituberculate, *Deltatheridium*. From the original specimen. Occlusion diagram by author.
- V. Lower Eocene. Primitive placental, *Didelphodus*. From the original specimen. Occlusion diagram by author.
- VI. Middle Eocene. Primitive primate, *Pronycticebus*. After Grandidier. Occlusion diagram by author.
- VII. Upper Eocene. Advanced tarsioid primate, *Microcharus*. After Stehlin. Occlusion diagram by author.
- VIII. Miocene. Primitive anthropoid primate, *Dryopithecus*. Upper molars mainly after Pilgrim; lower molars from type of *Dryopithecus cauleyi*. Occlusion diagram by author and Milo Hellman.
- IX. Pleistocene. Primitive man, Mousterian. From stereoscopic photographs by Professor J. H. McGregor and from the published photographs by Weinert and by Virchow (*m₃*). Occlusion diagram by author.
- X. Recent. Modern man, White. From the original specimen. Occlusion diagram by author.

tiveness. Our knowledge of them has been much extended in the past few years through expeditions sent out by Denmark, Sweden, Norway and by the personal explorations of the late Professor William Patten of Dartmouth College. Beautifully illustrated monographs and papers on the newly discovered ostracoderms have been written, especially by Kiaer and by Stensiö. In the typical ostracoderms, such as *Cephalaspis* and its allies, the head included a more or less semicircular "head shield," with a pair of eyes like spectacles, on top of the head shield. The interior of the head included a central chamber for the brain and a radiating system of tubes for the cranial nerves and the cranial arteries and veins. Below this level was the expanded mouth cavity containing on either side a diminishing row of about ten gill-pockets separated by skeletal septa. Natural casts of all these cavities and tubes were made by the infiltrated mud, which later turned to stone.

The close relationships of the ostracoderms to the existing cyclostomes (lampreys and hag-fishes) is now proved by the fact that the cranial nerves, arteries and veins of the larval lamprey find their unmistakable counterparts in the fossil ostracoderms described by Stensiö.

Likewise in the integument the ostracoderms exhibit a high degree of *polyisomerism*¹ within each system, joined with an equally high impression of *anisomerism*² when we see the parts of different systems side by side. The integument of the head-shield in the primitive Heterostraci or Pteraspido-morphi includes not less than four well differentiated layers, but each layer, as we pass from point to point within its boundaries, is composed of thousands of homogeneous units. Here we arrive at the basic fact that polyisomerism, whether primary or secondary, is always due to the multiplication, by budding, delamination or like processes, of embryonic

¹ The state in which there are many serially arranged homologous organs or parts of organs.

² The state in which the primitive polyisomeres have become reduced in number, either by fusion or by elimination, while some of those that remain have become overgrown or distorted.

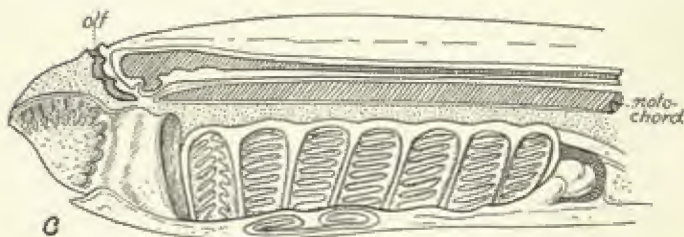
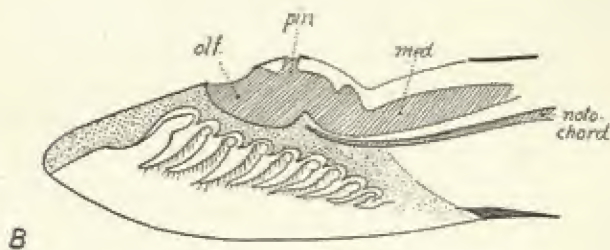
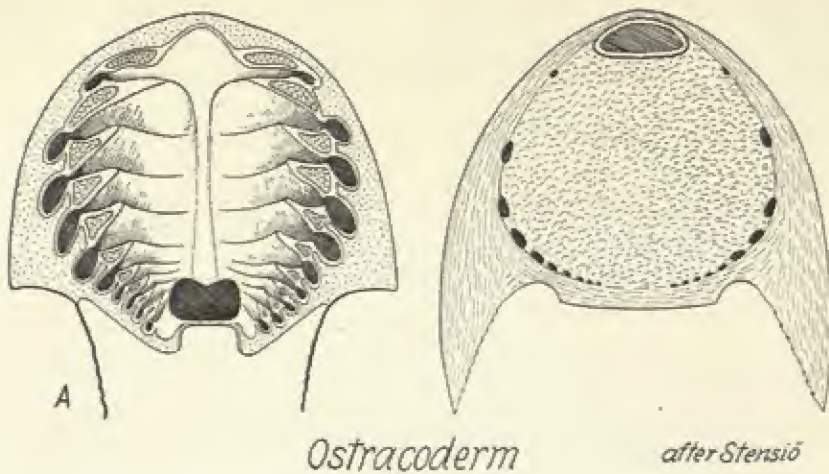
fundaments which may have started from some very much restricted locus and spread thence over wide areas.

While it is quite likely that the unknown chordates still earlier than the ostracoderms obtained their nutriment by the method of ciliary ingestion, it seems to be indicated that in the ostracoderms the rhythmic depression of the floor of the capacious mouth-cavity alternately drew in and expelled a supply of water through the small round mouth and minute circular gill-openings, thereby reinforcing perhaps the action of the cilia or bringing to them materials for selection, as in the endostyle of *Amphioxus* and the larval lamprey. The orobranchial series of pouches (Fig. 24) were arranged almost in a circle on the floor and sides of the mouth cavity and showed a high degree of primitive polyisomerism and a very gentle transition from one to the other. There were as yet no definite jaws, at least the jaw-bars, if any, were not yet differentiated from the septa between the gills and there were no teeth.

While the primitive cephalaspid ostracoderms (Fig. 25, B, E) were more or less flattened, bottom-living forms, their more progressive relatives the anaspid ostracoderms had acquired a stream-lined body-form and a good-sized tail-fin, suitable for the pursuit of small, actively swimming prey (Fig. 25, A). According to Kiaer, the genus *Rhyncholepis* had a median club-like epidermal plate in the front of the floor of the mouth, which may have served as a kind of primitive mandible.

In the recent lampreys (Fig. 26), which may be regarded as the specialized descendants of the cephalaspid ostracoderms, the body has become eel-like and the head reduced in size.

In connection with the habit of fastening on to the sides of living fish and rasping away pieces of the body wall, the buccal cavity of the adult lampreys has become enlarged and circular and provided with close-set rows of thorn-like horny teeth, while the so-called tongue (which may possibly represent the fused Meckel's cartilages of the shark) is armed with a movable rasp of sharp recurved teeth, somewhat analogous



Petromyzon larva

After Parker
& Goodrich

FIG. 24. The orobranchial region of cephalaspid ostracoderms and larval lamprey, representing the agnathous grade in the evolution of the vertebrate jaws.

A. Devonian ostracoderm. After Stensiö. The figure at the left is a reconstruction by Stensiö, from excellent material, of the roof of the mouth and under side of the head-shield. The future jaws are represented by the cartilaginous supports of one of the anterior gill-slits. The right-hand figure is a tentative restoration by Stensiö of the probable appearance of the under side of the mouth, gill-openings and related parts of another ostracoderm.

B. Thick sagittal section, after Stensiö, but with the position of the gills and gill-bars indicated.

C. Larval lamprey, sagittal section and inner side of branchial basket, showing agreement with ostracoderm in fundamental plan. Data from Goodrich.

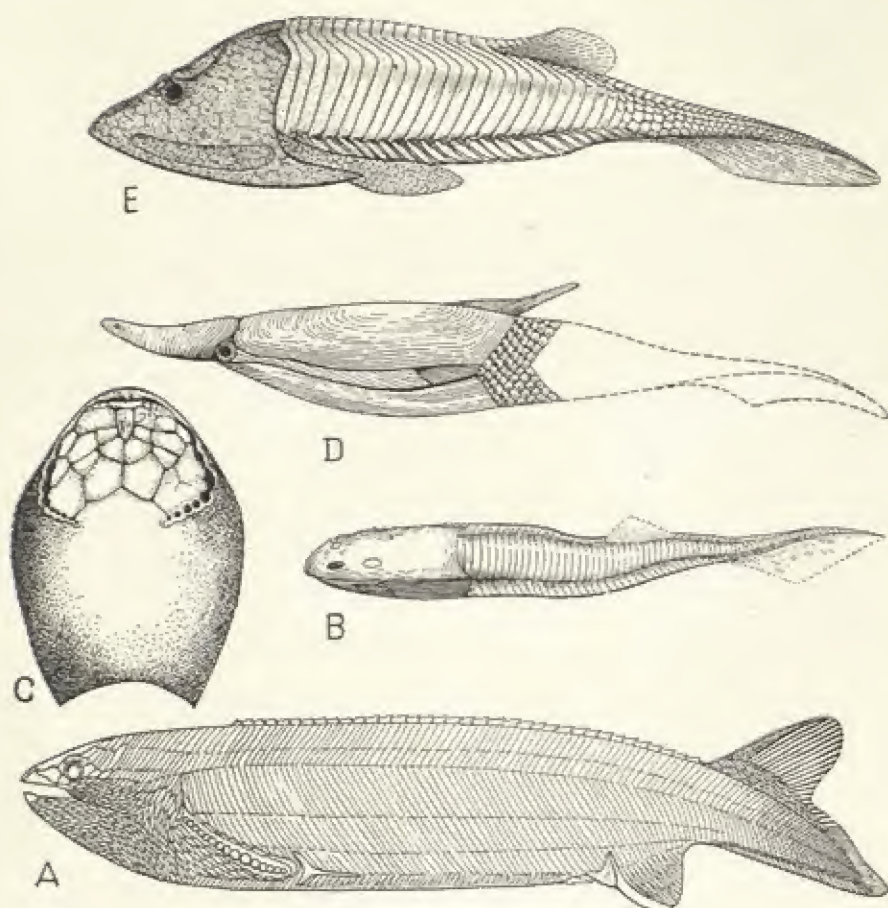


FIG. 25. Upper Silurian and Devonian ostracoderms. *A. Pharyngolepis*. (After Kjaer.) *B. Tremataspis*. (After Rohon.) *C. Tremataspis*. (After Patten.) *D. Pteraspis*. (After Powrie and Lankester.) *E. Cephalaspis*. (Composite, mainly after Patten.)

with the radula of gastropods. Both the numerousness and the simplicity of the teeth on the sides of the buccal funnel and on the "tongue" give at first sight the appearance of a primary polyisomerism, but the almost surely secondary nature of the feeding habits of the modern lampreys and the absence of these specializations in the known ostracoderms make the apparent primitiveness of the thorn-like, horny dentition of modern cyclostomes more than dubious.

Conodonts.—In some of the Devonian formations of Ohio and western New York there occur large numbers of minute calcified teeth called conodonts, which belonged to otherwise unknown creatures. Many authors have regarded these

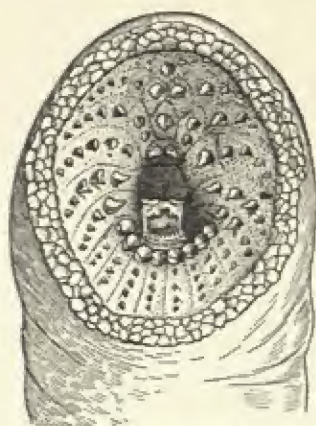


FIG. 26. The dental apparatus of the lamprey. After W. K. Parker. $\times 3/2$.

teeth as having come from the mandibles of aquatic annelids but recent investigators (Bryant, Miller) incline to the view that they belonged to primitive fish-like vertebrates probably related to the ostracoderms and therefore to the lampreys. If so, the more primitive conodont teeth (Fig. 27) appear to

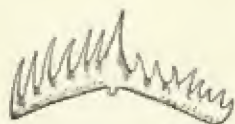


FIG. 27. Conodont from the Devonian. Much enlarged. After Holmes, 1928.

supply an almost ideally primitive condition of primary polyisomerism such as may be expected in the remote ancestors of the true jaw-bearing vertebrates.

Sharks.—A high degree of primary polyisomerism is retained in the dentition of many of the oldest known sharks and even in their modern descendants (Fig. 28 A, B). But it is only in a broad morphological sense that the shark, as

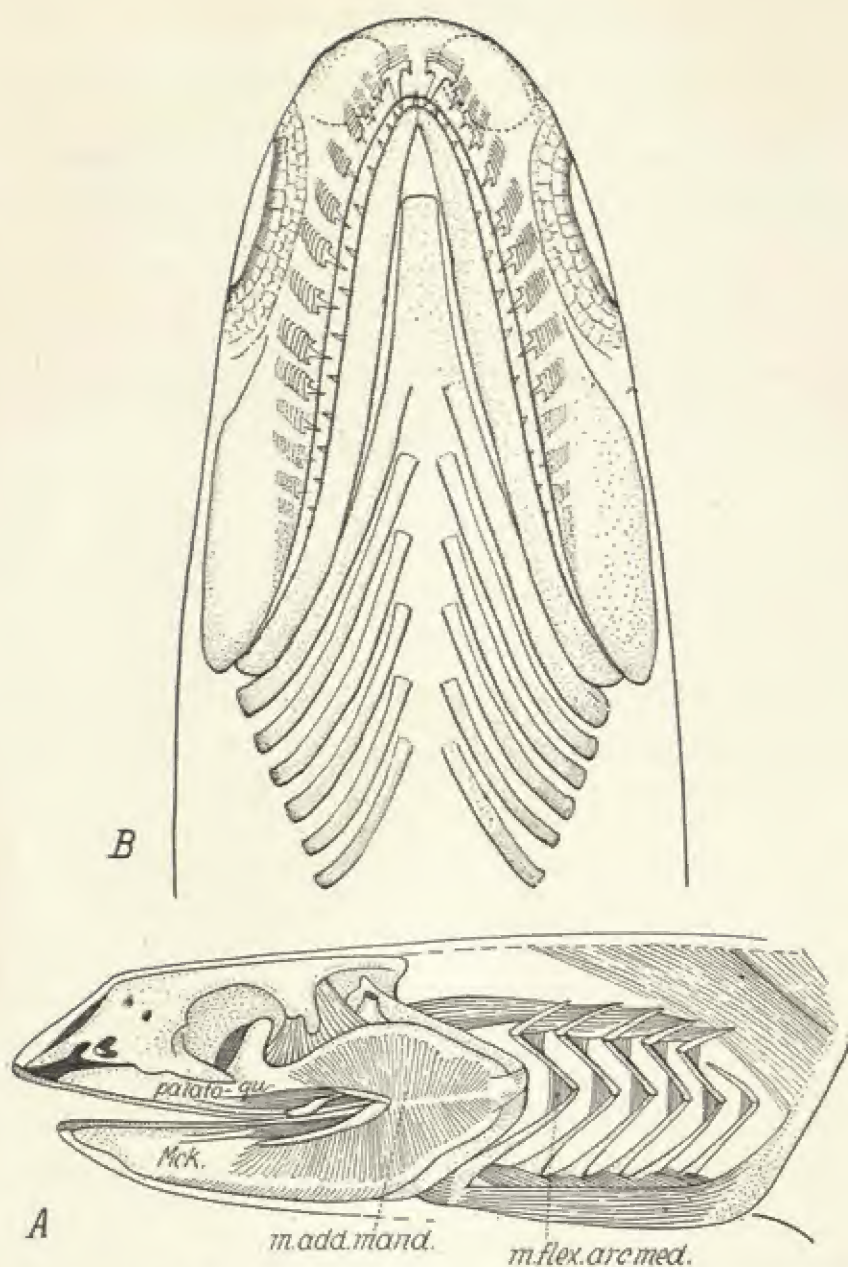


FIG. 28. *A.* The orobranchial skeleton and musculature of a modern shark (*Chlamydoselachus*). After Allis.

B. The orobranchial skeleton and musculature of an Upper Devonian shark (*Cladodus*). After Dean. Illustrating the primitive gnathostome grade of evolution of the vertebrate jaws. [Compare Fig. 24.]

represented by a modern shark, stands near to the general line of ascent to the higher vertebrates, since the real connection of the sharks with the higher vertebrates lies only through the as yet undiscovered ancestors of the palæozoic acanthodian sharks, which were in some respects intermediate between true sharks and the oldest forerunners of the ganoid fishes.

Spiral polyisomerism is the rule both in the predaceous sharks with sharp, jagged teeth, in molluscivorous, shell-crushing forms such as the Port Jackson shark (*Heterodontus*) and in the skates and rays, which have flattened teeth arranged in whorls or tessellated pavements.

The successional teeth of sharks (Fig. 29) are likewise highly polyisomeric, especially if we compare the members of a single spiral successional series (see p. 218). They are covered on the lingual side by an operculum or fold of the mucous epithelium.

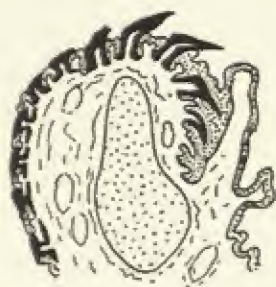


FIG. 29. Successional teeth of shark. Cross-section of lower jaw showing development and succession of teeth in *Scyllium canicula*. After Goodrich.

True Ganoids and Lobe-fins.—In the line leading to the higher vertebrates the dental lamina at an early stage of embryonic development sank into a groove and was covered by the sheathing bones called respectively dentary in the mandible and premaxilla and maxilla in the outer upper jaw, while dentigerous plates were spread upon the anterior and posterior coronoids in the mandible and upon the prevomers, palatines, pterygoids and ectopterygoids of the inner upper jaw. This was the stage already attained in the earliest known

true ganoids (cheirolepids) and lobe-finned ganoids (crossopterygians) of the Old Red Sandstone of Great Britain and equivalent Mid-Devonian formations of North America. In the crossoptrygians the large teeth on the inner side of the mandible and on the lateral parts of the upper jaw were fastened to their bony supports by the deep and complex infolding of the bases of the teeth and the bony tissue upon which they rested. This is an excellent example of intradental polyisomerism. The labyrinthodont tooth (Fig. 30) and the labyrinthodont mode of attachment were far older and more primitive than the other more widely known kinds of teeth and modes of attachment, including the pleurodont and acrodon types in lizards and the thecodont type in the ancestors of the mammals.

Teleosts.—Perhaps ninety per cent of the existing species of fishes belong to the advanced subclass of teleosts, which gradually crowded out the ganoids in the latter half of the Age of Reptiles. The teeth on the marginal jaw-bones (premaxillæ, maxillæ, dentaries) are usually small and pointed; occasionally they develop on the one hand into sharp, dagger-like teeth (*Barracuda*, Fig. 31 A); at the other extreme we may find incisor-like teeth in front and pebble-like molar teeth on the sides, as in the sheep's-head (Fig. 31 B). The aggregation and coalescence of large numbers of tooth germs may give rise to a powerful parrot-like beak, as in the puffers (*Spheroides*) and porcupine fishes (*Diodon*, Fig. 32 A). But the most remarkable modifications are seen in the pharyngeal teeth borne on specially enlarged segments of the posterior gill-arches, which in the parrot-wrasses (Fig. 32 D) finally include upper and lower rasp-like strips, each arranged in rows of flattened oval or narrow V-shaped columns and operated by powerful muscles. It may be said that in the dentition of the teleosts the rule of local polyisomerism has few exceptions. Rarely, extreme differential growth results in the enormous size of one pair of curved needle-like teeth, as in *Chauliodus*.

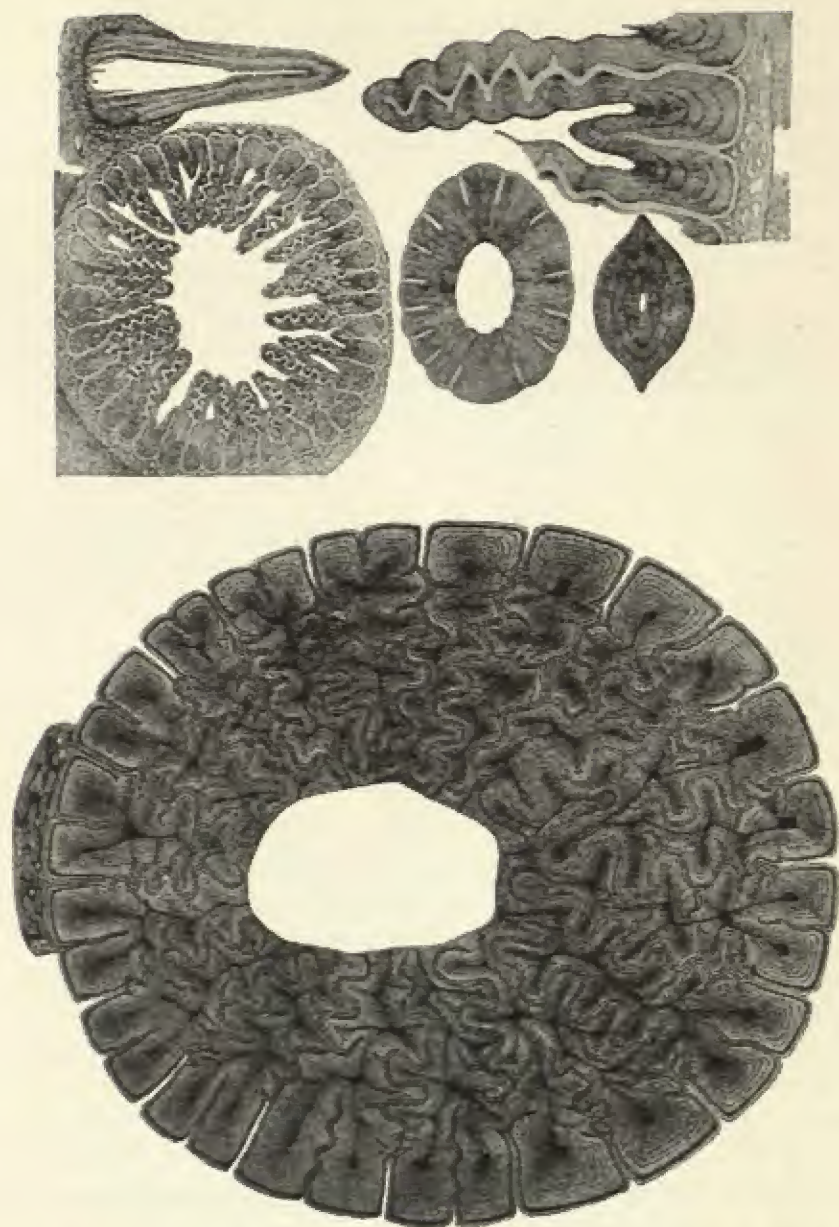


FIG. 30. Upper figures: cross-sections of labyrinthodont teeth, illustrating the complexly infolded base characteristic of *Loxomma allmani*, one of the earliest amphibians. After Embleton and Atthey.

Lower figure: Cross-section (enlarged) of tooth of *Polyplocodus*, a lobe-finned Devonian fish. After Pander.

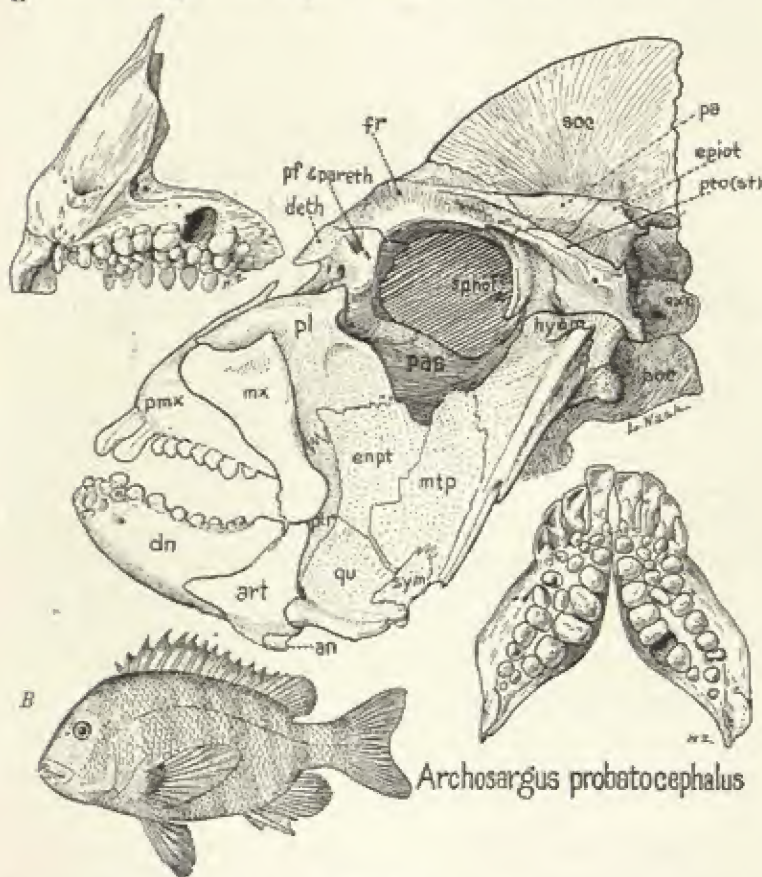
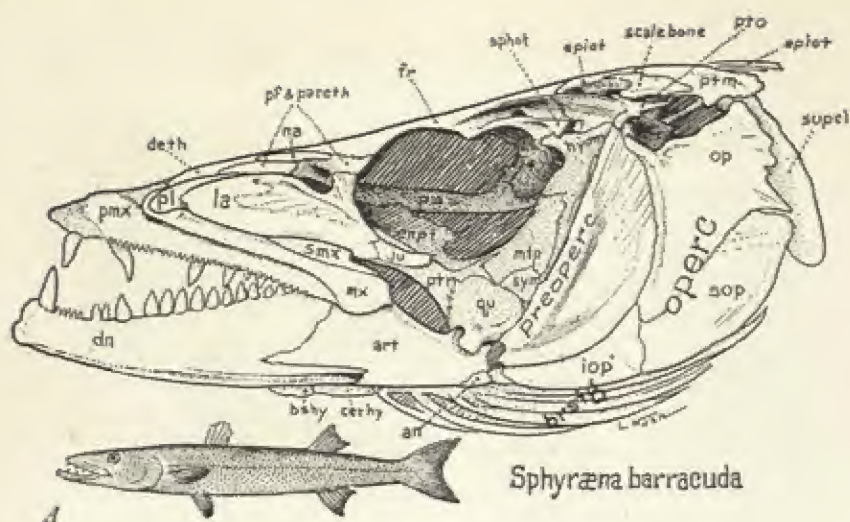


FIG. 31. Contrasting dentitions of (A) barracuda (*Sphyræna*) and (B) sheepshead (*Archosargus*). After Gregory, 1933.

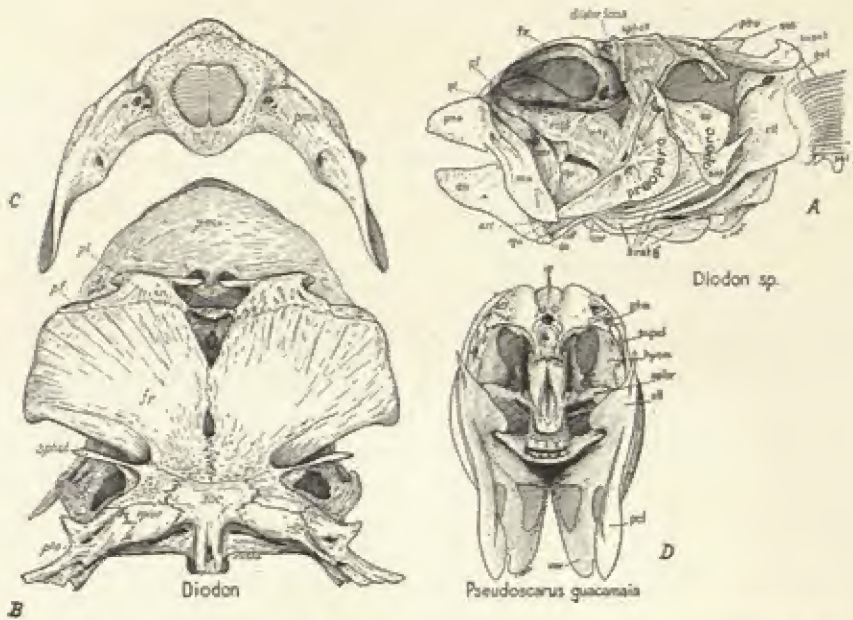


FIG. 32. A, B, C, skull, beak and crushing jaws of *Diodon*. D, pharyngeal dental apparatus of parrot-wrasse (*Scarus*), seen from the rear. After Gregory, 1933.

Earliest Amphibians (Stegocephs).—The earliest known tetrapods, which are the newly discovered stegocephalians of the Upper Devonian of East Greenland described by Dr. S  ve-S  derbergh (1932), retain the full complement of jaw-bones established in the crossopterygians, together with the labyrinthodont teeth. Even in the descendants of these forms (Fig. 33) as well as in the ancestral crossopterygians, there is a high degree of primitive but local polyisomerism if we compare single teeth with others belonging to the same region, such as those borne by the dentary or the set of large teeth borne by the coronoids. There is also a high degree of primitive polyisomerism when we compare corresponding teeth of the upper and lower jaws.

Aberrantly Specialized Reptilian Dentitions.—From the facts set forth in the previous section it will be realized that a state of primitive polyisomerism that was characteristic of the dentition of the earliest true fishes often gave rise to anisomer-

ism or differentiation and that this condition in turn may either become progressive, giving rise to more and more differentiated parts, or through the further budding of both

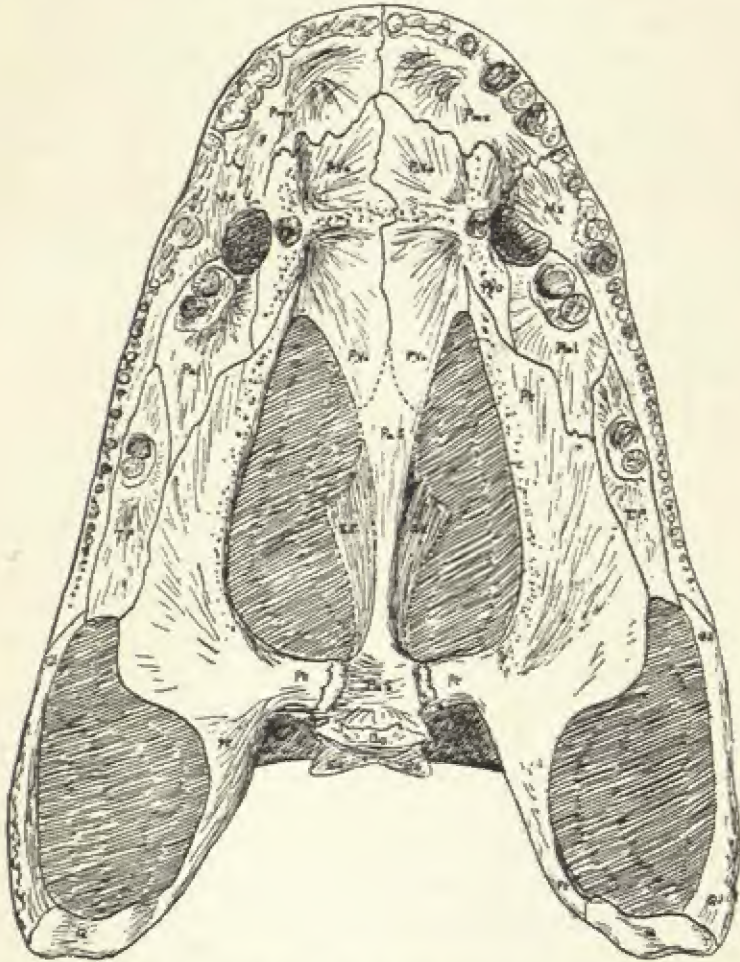


FIG. 33. Palate of *Eryops megacephalus*, a stegoceph from the Permian of Texas. One fourth natural size. After Broom.

anisomeres and polyisomeres we may see a process of secondary polyisomerism, as in the teeth of pikes.

The primitive polyisomerism of the most ancient true fishes persists throughout all generalized amphibians and early

reptiles but in the later reptiles it gives way usually to anisomerism of the dentition as a whole and often to a marked secondary polyisomerism of certain regions of the dentition.

Of the hundreds of known species of fossil and recent amphibians and reptiles the specializations of the dentition alone are sufficient to rule most of them out of the line of ascent to man, if we admit, as seems necessary, the validity and applicability of Dollo's Law of the Irreversibility of Evolution. Let us first review briefly then the main classes of specialization of the dentition of recent and fossil reptiles, except the mammal-like reptiles, which will be considered in the following section.

(1) Ancestral stage of polyisomerism. Perhaps the most primitive condition is found in the Permo-Carboniferous *Seymouria*, which stands near the line between the earliest fossil amphibians and generalized reptiles. In this form the "marginal teeth" on the outer upper jaw are numerous and simple, probably with infolded labyrinthodont bases. In *Captorhinus*, a relatively primitive cotylosaur, there are numerous small teeth in several rows on the marginal jaw-bones and patches of fine teeth on the roof of the mouth. In the primitive theromorph *Mycterosaurus* the marginal teeth are primitive and relatively polyisomeric (Fig. 34 A), but with incipient regional anisomerism.

(2) Secondary polyisomerism due to multiplication of numerous pencil-like or slightly recurved pointed teeth set in parallel rows in a very long bony rostrum. Is often associated with fish-catching habits, as in ichthyosaurs (B), marine crocodiles, phytosaurs, etc. Here longitudinal polyisomerism results from long continued horizontal and vertical budding of the dental lamina.

(3) Regional polyisomerism of the front teeth, which are developed as a scoop, the posterior teeth reduced or absent, as in *Diplodocus* (C).

(4) Marked local anisomerism in the cheek teeth, which are reduced to a single pair of large poison fangs pierced by a canal and connected with the poison glands, hinged and

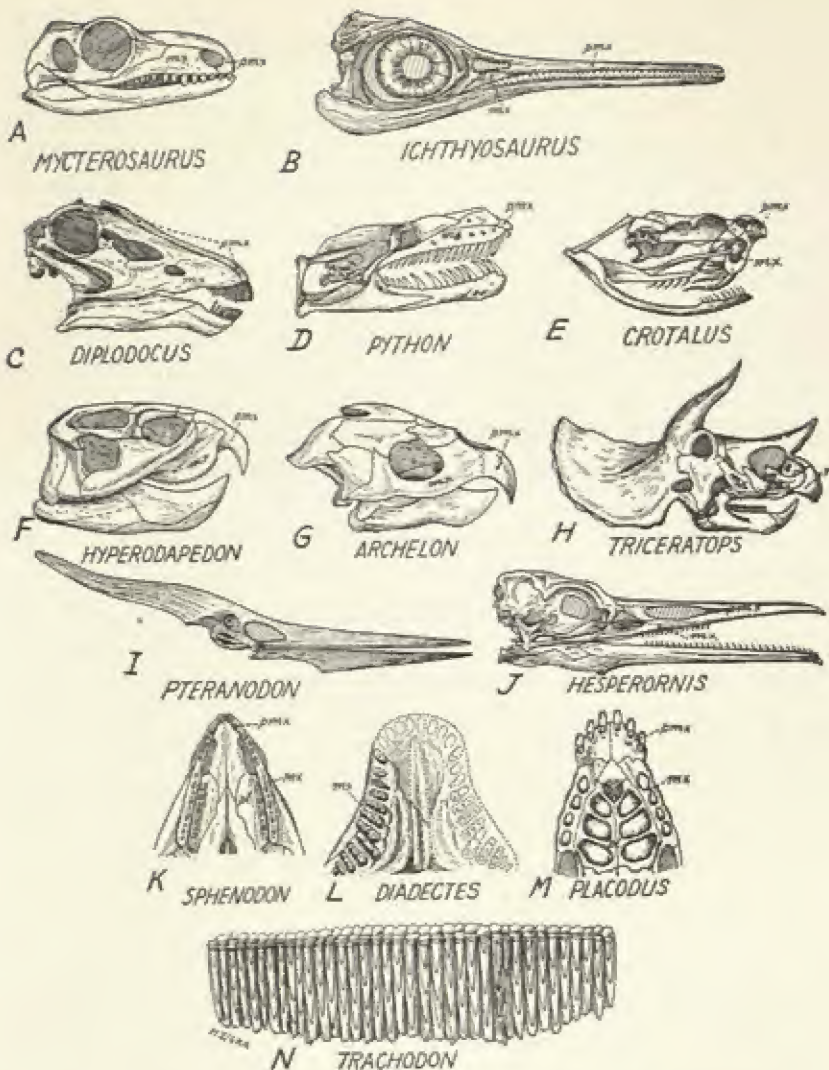


FIG. 34. Adaptive radiation of the dentition in the Reptilia. Scales various.

- A. *Mycterosaurus*, Order Theromorpha. After Williston.
- B. *Ichthyosaurus*. Order Ichthyosauria. After E. Fraas.
- C. *Diplodocus*, Order Saurischia, Suborder Sauropoda. After Hatcher and Holland.
- D. *Python*, Order Squamata, Suborder Serpentes. Partly after Williston.
- E. *Crotalus*, Order Squamata, Suborder Serpentes. After Zittel.
- F. *Hyperodapedon*, Order Rhynchocephalia. From Zittel.
- G. *Archelon*, Order Chelonio. After Wieland.
- H. *Triceratops*, Order Ornithischia, Suborder Ceratopsia. After Marsh.
- I. *Pteranodon*, Order Pterosauria. After Eaton.
- J. *Hesperornis*, Order Odontornithes. After Marsh.
- K. *Sphenodon*. Order Rhynchocephalia. After Romer.
- L. *Diadectes*. Order Cotylosauria. Partly after Case.
- M. *Placodus*. Order Sauropterygia. After Zittel.
- N. *Trachodon*. Order Ornithischia, Suborder Orthopoda. After Barnum Brown.

TABLE I
ADAPTIVE RADIATION OF MARGINAL DENTITION OF REPTILES

Group	Types	Primitives Polyisomeres		Anisomeres		Secondary or Hyperpolyisomeres		Anodontian (Loss of Teeth)	
		Front Teeth	Cheek Teeth	Front Teeth	Cheek Teeth	Front Teeth	Cheek Teeth	Front Teeth	Cheek Teeth
COTYLOSAURIA	<i>Scymnouria</i>	x	x						
THEROMORPHA	<i>Diadectes</i>			x	x ¹				
ICHTHYOSAURIA	<i>Myctrosaurus</i>	x	x						
	<i>Ichthyosaurus</i>					x ²	x		
	<i>Rapianodon</i>								
SAURISCHIA	<i>Platosaurs</i>	x	x						
	<i>Diplodocus</i>					x			
	<i>Python</i>	x	x						
SQUAMATA	<i>Crotalus</i>				x			x	
	<i>Youngina</i>	x	x						
RYNCHOCEPHALIA	<i>Sphenodon</i>			x			x		
CHelonIA	<i>Eumelosaurus</i>	x(?)	x(?)						
	<i>Chelone</i>							x ³	x ³
ORNITHISCHIA	<i>Hypsilophodon</i>	x	x					x ³	
	<i>Trachodon</i>						x		
SAUROPTERYGIA	<i>Nothosaurus</i>	x	x						
	<i>Placodus</i>			x			x ⁴		
THEIODONTIA	<i>Eumatheria</i>	x	x						
	<i>Cynognathus</i>			x	x ⁴				
ANOMODONTIA	<i>Galpus</i>	x	x						
	<i>Lyttosaurus</i>							x ³	x ³

¹ Wide oval crowns; ² rostrum elongate; ³ horny beak present; ⁴ crushing molars; ⁵ cuspidate.

erectile as in the vipers (E). This condition has been derived by extreme anisomerism from the relative polyisomerism retained by the python (D).

(5) Regional anisomerism associated with loss of front teeth and development of a horny beak by hardening and extension of the gums, as in rhynchosaur (F), chelonians (G) beaked dinosaurs (H), the later pterosaurs (I), also in the birds (J), where the beak at first does not replace the lateral teeth.

(6) Longitudinal agglutinative polyisomerism, producing long serrated blades due to coalescence of conical teeth, as in *Sphenodon* (K).

(7) Regional anisomerism, with development of thick procumbent incisors and huge rounded, secondarily polyisomerous molar masses on the roof of the mouth and inner sides of the mandible, as in the "durophagous" placodonts (M).

(8) Regional anisomerism involving the development of a duck-like beak in front and of one or more closely appressed rows of originally spatulate, serrate cheek teeth, as in *Camptosaurus*.

(9) Excessive secondary polyisomerism of the successional teeth, agglomerated into four massive dental batteries containing in all over two thousand teeth, as in *Trachodon* (N), a highly efficient grinding mechanism for cutting tough vegetation.

(10) Regional anisomerism involving development of partly procumbent incisors and transversely widened oval molars with a central cusp alternating with transversely ridged lower molars, as in *Diadectes* (L).

Adaptive Radiation of the Dentition in the Mammal-like Reptiles.—Thanks to Doctor Broom's excellent work (1932) on the Mammal-like Reptiles of South Africa, with its abundant and skilfully drawn figures, the reader may easily acquire a general view of the adaptive radiation of the dentition in this immensely diversified group as summarized in Figs. 31, 32, which are based on Doctor Broom's drawings.

These mammal-like reptiles on the whole leaned toward a protein diet supplied by living prey but, as in other groups of carnivores, the predators were followed by numerous carrion feeders and these in turn were outnumbered by the more adaptable "general feeders," in this case the beaked anomodonts; these from their vast numbers and diversity, could presumably make use of almost any kind of food, animal or vegetable.

We start then with the undifferentiated polyisomeric teeth of the smaller theromorphs such as *Eumatthevia* (Fig. 35 A) of the Lower Permian of Texas, and *Anningia* (B) of the Middle Permian of South Africa, which have recurved conical teeth on the margins of the jaws. Among the oldest of the mammal-like reptiles of South Africa are the Dinoccephalia and of these the titanosaurs (C), some of which attained the size of hippopotami, are regarded as carnivorous because they retain the canines; their close relatives the tapinocephalids are regarded as herbivorous because the canine is not enlarged while the incisors are enlarged and partly spoon-shaped, presumably for plucking up tough vegetation.

Perhaps the first step toward the beak-like anomodonts is seen in the little short-faced *Galepus* (Fig. 35 D), whose zygomatic arch might have folded up into the peculiar inverted V that is characteristic of the anomodonts. Among these the genus *Pristerodon* retained about twelve well developed molars on each half of the mandible. According to Broom (*op. cit.*, p. 213), each of these teeth "has a high flattened crown with a series of large serrations on the posterior edge. There is probably a dental succession in the molars." In *Dialurodon* (*op. cit.*, p. 216) there were also small molars. In some of the typical endothiodonts (Fig. 35 E) a row of small conical molars was retained on the inner side of the maxillæ medial to the beak. The males in many anomodonts retained a pair of very large canine tusks, a circumstance to which the name *Dicynodon* alludes, while the females lack tusks and hence were long called *Oudenodon*. In *Lystrosaurus platyceps*, a late survivor of the group, the beak becomes

sharply deflected downward and the face was somewhat like that of a walrus. Thus the dentition in the later anomodonts is extremely anisomerous.

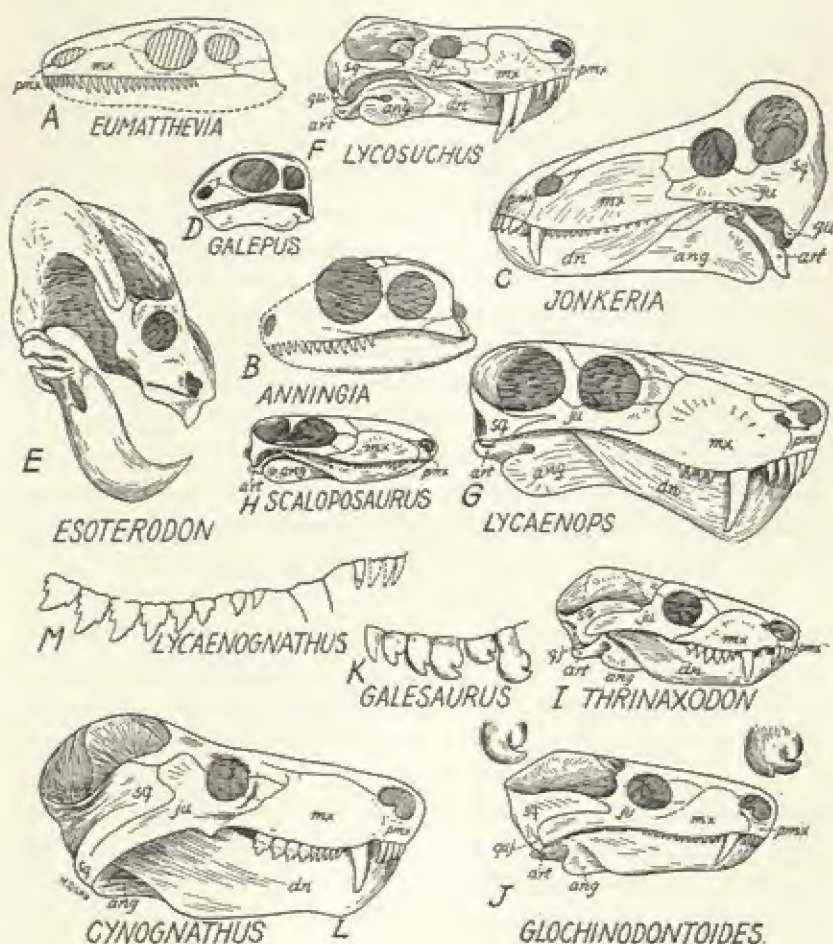


FIG. 35. Adaptive radiation of the dentition in the mammal-like reptiles. Scales various. All figures after Broom.

In another direction the primitive polyisomerous therapsids gave rise to the earlier therocephalians (Fig. 35 F), which were active predators, often with two enlarged canines on each side, very small molars and vertical piercing incisors. The

gorgonopsians (G) were much like the earlier therocephalians in their dentition, except that there was only one pair of canines.

In some of the small later therocephalians (H) the post-orbital bone was lost, as in the earliest mammals, but the dentition was polyisomeric and truly generalized. A similar advance in the postorbital region is seen in the Bauriamorpha (Fig. 36 A), in which the closely appressed, transversely oval teeth foreshadow those of some of the most advanced therapsids, the ictidosaurians (Fig. 36 M).

Doctor Broom (1932, p. 77) states that in one small therocephalian named *Cyrbasiodon boycei* the maxilla bore a series of about thirteen molars, of which the sixth has "a large main cusp and when viewed from without, very small anterior and posterior cusps. On the inside there is a feeble cingulum, which has two small inner cusps. The seventh tooth is evidently a replacing one and only the main cusp is seen. The eighth and ninth teeth are like the sixth but with a more marked inner cingulum and larger internal cusps. The tenth tooth has the main cusps less developed and the posterior cusps also smaller. The eleventh tooth is still smaller."

This is one of the earliest indications of the process called "cuspidation," together with the formation of a cingulum and of cingulum-borne cusps, which was destined to play a commanding part in the evolution of the molar teeth of mammals. But let us pause for a moment to consider what is involved in these processes. Cuspidation I take to be due to the concentration within the boundaries of a single tooth germ of some of the power to bud which was formerly diffused more widely over the whole dental lamina. In other words, cuspidation is the beginning of intradental polyisomerism, which often comes after interdental polyisomerism.

When a cusp grows out from a crown it must be the locus of higher growth pressure, just as is the growing tip of an onion. Since the cingulum is only a projecting ledge around the base of a crown, the transverse growth in the plane of

that base must be faster than the vertical growth. This is probably the reason why basal cingula are usually most conspicuous on very low-crowned teeth, while on high-crowned teeth they are either inconspicuous or else sometimes share the vertical growth and take part in the formation of crests and folds.

But not to run too far ahead of our story let us return to this lowly Permian therocephalian *Cyrbasiodon*. It will be noted from Doctor Broom's description that "the eighth and ninth teeth are like the sixth but with a more marked inner cingulum and larger internal cusps. The tenth tooth has the main cusps less developed and the posterior cingulum also" smaller. The eleventh tooth is still smaller." Here we have an instance of the progressive emphasis of the cingulum and of its secondary cusp as we pass backward to a sort of anticlinal tooth behind which the size and complexity rapidly decline. Thus we have to a certain extent a foreshadowing in the Permian period of the process of premolar complication and of anticlinal development which can be so clearly observed in the cheek teeth of many families of mammals in the early Eocene. Since as a rule the characters of the lower teeth are closely correlated with those of the upper, so as to produce an efficient mechanism, we may expect that the internal cingulum cusps of the upper molars of *Cyrbasiodon* will be found to receive or occlude with the labial side of the tip of the lower molars, which may also have an external cingulum.

The tendency toward cuspidation is very clearly expressed in the cynodont suborder of the Therapsida. These remarkably mammal-like skulls (Fig. 35 I-M) have four kinds of teeth: incisors, canines, premolars and molars, and the present evidence suggests that there were but two sets of teeth in the ante-molar cheek teeth and only one set in the molars. In all these forms the dentary was becoming enlarged and the small jaw-bones behind the dentary were becoming reduced, so that the jaw was approaching the mammalian stage, involving the establishment of a dentary-squamosal articulation. In some of the smaller cynodonts (Fig. 35 I) the

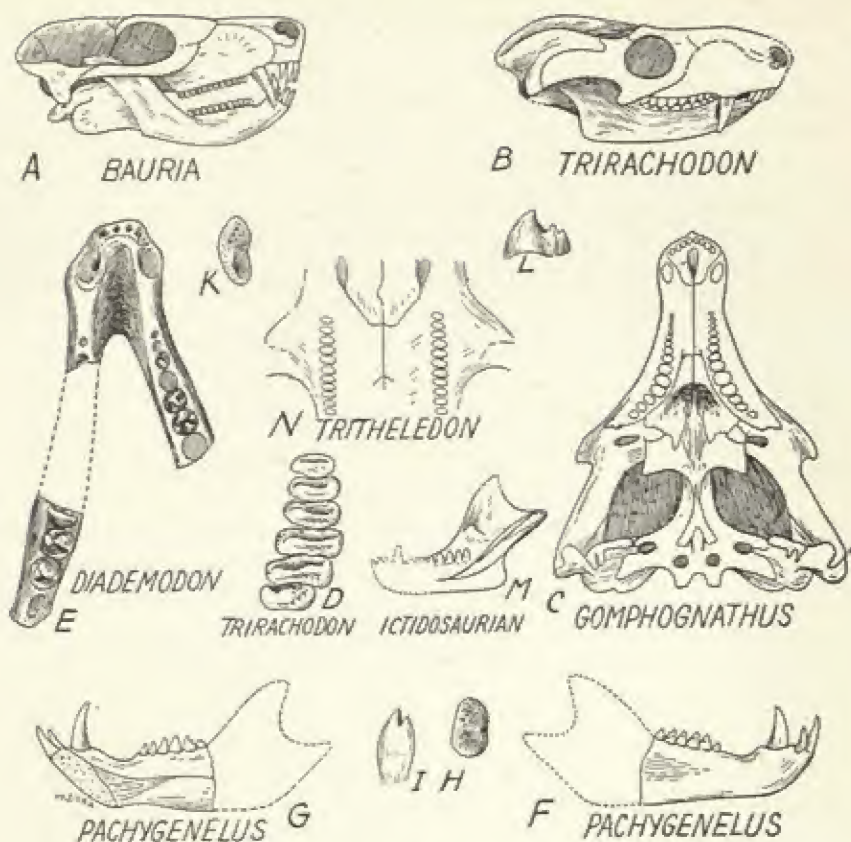


FIG. 36. Adaptive radiation of the dentition in the mammal-like reptiles (continued). Scales various. All figures after Broom.

Perhaps the only figures that require special notice are the following:

- D. Left upper cheek teeth of *Trirachodon*.
- E. Crown view of lower dentition, showing empty alveoli of some of the deciduous teeth and tips of certain replacing teeth (e.g., canines, premolars) lying deep beneath the deciduous teeth.
- F. Outer side of mandible of *Pachygenelus*.
- G. Inner side of mandible of *Pachygenelus*, showing that the highest cusps of the molar crowns are on the lingual side.
- H. Crown view of fifth left cheek tooth. The largest cusp is anterior in the jaw.
- I. Back view of fourth lower molar of the same animal.
- K. Fifth left upper cheek tooth of *Tritheledon*; crown view showing transversely widened crown with highest cusp on the outside.
- L. Anterior view of eighth left upper tooth of *Tritheledon*.

dentition also closely approached the most primitive mammalian type. In others (J, K) the upper molar crowns were curiously recurved and expanded with a bilobed tip of unknown functional value. In the large cynodonts (L, M) the predatory dentition reached its climax and the cheek teeth from front to rear exhibit successive stages in the development of jagged, many-cusped shearing blades.

While the carnivorous cynodonts were, so to speak, making a strenuous but apparently unsuccessful effort to rise above the reptilian class, their close relatives the gomphodont division of the Cynodontia (Fig. 36 B, C, D) were also slowly arriving at certain "basic patents" in the occlusal relations of the upper and lower teeth which, while perhaps not directly transmitted to the mammals, yet showed the way, as it were, for the ancestors of the mammals to follow. For the gomphodonts achieved three marked advances in the mammalian direction: first, they widened the upper cheek teeth transversely and progressively from the premolars to the anticlinal tenth molar; second, they developed rounded cusps and low transverse ridges on the upper molars, which alternated with smaller ridges and cusps on the lower molars; third, they did not develop both upper and lower molars alike; so that instead of upper and lower teeth being merely reversed copies of each other, as in the earlier reptiles, the gomphodonts acquired almost mammalian occlusal relations of the upper and lower cheek teeth merely by stressing the transverse growth plane in the upper teeth and a slight transverse ridge on the circular-crowned lower molars (Fig 23 II, p. 210).

The latest of the mammal-like reptiles, from the Red Beds of the Stormberg in South Africa, are known from tantalizingly incomplete but highly important fragments, which are provisionally referred to the suborder Ictidosauria by Broom (1932, pp. 299-307). In one of them, named *Pachygenelus* (Fig. 36 F-I) by Watson, the fifth lower molar crown had relatively high main inner cusps margined by two lower posterior cusps, together with a strong external cingulum bearing one low elevation or incipient cusp. Here then is a

case where the principal tip of the lower molars lies on the inner or lingual side of the crown, as it possibly did in the multituberculates among the mammals.

In another form, *Tritheledon* (Fig. 36 N), the upper molar crowns formed transversely extended ovals, and an anterior view of the fifth left upper molar (L) revealed a high outer cusp and two low cingulum cusps in a transverse sequence, so that there were three transverse cusps in such a molar. From the straightness of the tooth row and enormous size of the muzzle it would seem that this animal suggested the contemporary *Tritylodon* multituberculates before the molar crowns became secondarily elongated anteroposteriorly. *Tritheledon* may thus have been an archaic form suggesting an early stage in the direction of *Tritylodon* without being actually ancestral to it.

By far the most advanced of the mammal-like reptiles were the small forms from the Stormberg called Ictidosaurians A and B by Broom. The skulls were almost mammalian in general construction and the lower jaw (Fig. 36 M) was so far advanced that the bones behind the dentary were greatly reduced, while the new dentary-squamosal contact was very nearly effected by a posterior process of the ascending branch of the dentary. The lower cheek teeth were closely appressed, transversely oval, "with a powerful main cusp and a second cusp on its outer side and there is a rudimentary cingulum round the base" (Broom, 1932, p. 301). They probably fitted between the oval upper crowns. The elevation of the ascending ramus of the mandible is greater in these forms than it was in the most primitive mammals, so that these Ictidosaurian A and B skulls may perhaps be rather the grand uncles than the direct great grandfathers of the later mammals.

In conclusion, the lower mammal-like reptiles are primitively polyisomeric in their dentition but within each tooth there is but little differentiation. In the higher mammal-like reptiles the dentition is, on the whole, intermediate in various ways between the primitive polyisomerism of the older

Permian theromorphs and the low grade regional anisomerism of the typical mammals with cuspidate shearing cheek teeth.

The gomphodont members of the cynodonts point the way to a "basic patent" of the primitive mammalian dentition in so far as they effected a transverse widening of the upper molars and a fitting of this internal ridge between successive lower teeth. The latter, however, were crowded and their crowns not yet sufficiently spaced, nor had their posterior basal parts begun to elongate anteroposteriorly as they did in the typical mammals.

The little known Ictidosauria, in spite of the advanced submammalian stage of their skulls and jaws, seem to have foreshadowed not the typical mammals but at most only the tritylodont division of the multituberculates, in so far as they had developed three transverse cusps in the upper and two in the lower molars but without having yet elongated the molars anteroposteriorly.

Adaptive Radiation of Molars in Mammals, with a Critique of Friant's Theory

The "Protodont" Dentition.—Two famous little fossil jaws (Fig. 37) preserved on slabs of Upper Triassic coal in North Carolina were taken by Osborn to be the sole known representatives of a hitherto unknown order, which he named the Protodonta. Dr. G. G. Simpson, however, has recently given convincing evidence that these jaws do not represent an otherwise unknown group but are American representatives of the cynodont division of the mammal-like reptiles. Nevertheless their dentition is of extreme interest for just that reason, since the higher mammal-like reptiles, to judge from the construction of their entire skeleton, stood very near to the origin of the mammals.

The "protodont" dentition, as it may still be called, is characterized by its regional differentiation into incisors, canines, premolars and cuspidate molars. All these teeth were borne solely by the dentary, while the several elements behind the dentary must have been of small size, as they are

in other late cynodonts, preceding the final development of the dentary-squamosal joint in mammals. The incisors (three on each side) were simple, erect, pointed, showing no trace of the double triconodontism attributed by Professor Bolk, at least as a potentiality, to all early mammalian teeth. The small pointed incisors, erect canines, the simple styloid premolars and incipiently triconodont molars all testify to the animal diet of the protodonts, which possibly fed on insects. These

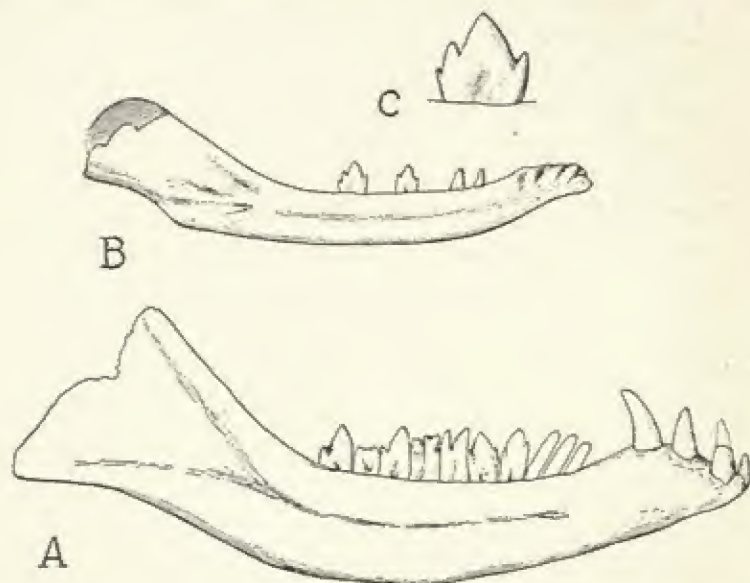


FIG. 37. *A. Dromatherium*, lower jaw. $\times 4$. *B. Microconodon*, lower jaw. $\times 4$. *C. Microconodon*, single molar. $\times 12$. All after Simpson, 1926.

forms were already far removed from the simple polyisomerism of primitive reptiles, which had numerous simple conical teeth; but the anisomerism of the dentition as a whole in the Protodonta had been attained *pari passu* with a local incipient polyisomerism within the molars, a phenomenon widely seen among the mammals.

It has been noted in the previous chapter that the advent of the process called cuspidation in the mammal-like reptiles was an event of great importance from the point of view of the

history of the dentition in the mammals. It would seem as if the force which normally gave rise to a single tip sprouted and gave rise to accessory cusps on either side of the main tip. Here is the beginning of the phenomenon of intradental polyisomerism, which becomes very highly and individually developed in many mammalian phyla.

The Triconodont Dentition.—Although the Jurassic triconodonts are by definition true mammals, since they already possessed the paired dentary-squamosal joints that are the accepted insignia of mammalian rank, they may or may not have been derived independently of the later mammals from the higher mammal-like reptiles. The idea of Cope and Osborn that they were directly ancestral to the later mammals and that their molar teeth were prototypal to those of all mammals has not been supported by satisfactory evidence and has been abandoned or held to be *sub judice* by Dr. George Gaylord Simpson, the author of many important works on the Mesozoic and later mammals. Nevertheless the triconodont dentition (Fig. 38) exhibits a considerable number of characters which we have every reason to regard as prototypal to those of later and more typical mammals. The dentition was heterodont (anisomorous) and carnivorous in type, with differentiated incisors, canines, premolars and cuspidate molars; it was also diphyodont. The jaw movement was more or less vertically shearing (true orthal type), with the condyle slightly below the level of the cheek teeth as in primitive carnivorous dentitions. The upper tooth row hung outside of the lower tooth row, so that the upper molars wore down on the inner side, the lower on the outer side, while one lower molar articulated with two upper molars. There was a heavy external cingulum on the upper molars and an internal cingulum on the lower molars; the molar teeth had two well separated roots arranged in an anteroposterior plane—all these features reinforcing the strong cuspidation of the molars in establishing the fully mammalian status of the triconodonts.

Among the dentitions of the higher mammals a marked degree of resemblance to the triconodont type is to be found in the carnivorous dentitions of certain seals (*Lobodon* and *Phoca gichigensis* Allen), but there is strong reason for regarding this as a pure convergence associated with similar food.

General regional anisomerism in the triconodonts is apparently a very early mammalian character, but in these

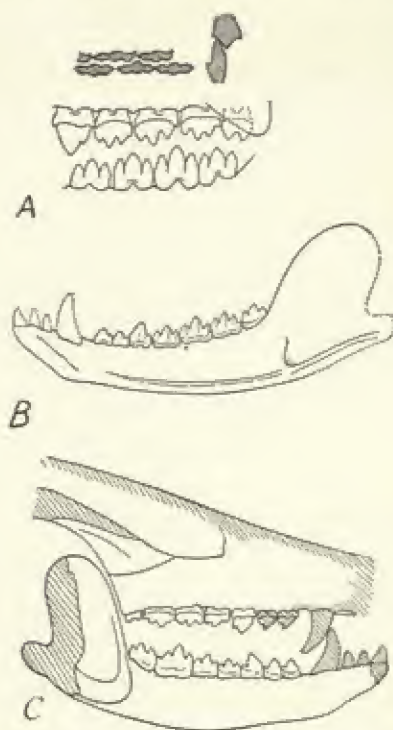


FIG. 38. Jaws and face of a typical triconodont, *Priacodon*. $\times 3/2$. After Simpson.

forms there was already an incipient secondary polyisomerism in so far as the posterior deciduous premolars were molariform, while in the permanent premolars the molar pattern was only incipient, the accessory cusps being but slightly developed. Thus whether or no the triconodonts were off the direct mammalian line, they assuredly lend support to the premolar analogy theory that the molars were at one time like the

simplest premolars, as indeed the molars are in the earliest mammal-like reptiles. In the more primitive triconodonts there were five small lower molars (on each side) but in the very advanced *Trioracodon* there were only three large molars (Simpson, 1928, Fig. 19, p. 68); this suggests the somewhat similar reduction in the trituberculates, when a larger number of small molars was gradually reduced to a smaller number of large molars.

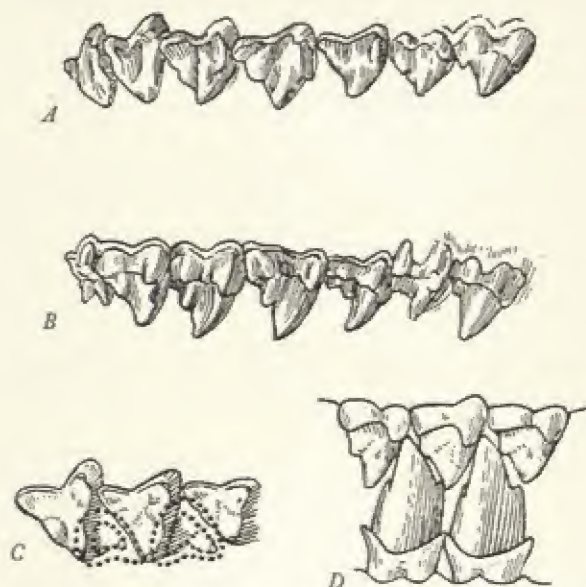


FIG. 39. Cheek teeth of symmetrodonts. After Simpson. *A, B. Peralesites*, crown and outer views. $\times 6$. *C, D. Peralesites*, upper, in occlusion with *Spalacotherium*, lower, molars. *C*, crown view; *D*, outer side view.

The Symmetrodont Dentition.—The symmetrodonts, very small mammals from the Jurassic of England and Wyoming, have recently been separated by Simpson (1925, p. 560; 1928, p. 97) on the one hand from the triconodonts and on the other from the trituberculates (pantotherians), with which they had been confused by earlier authors. They are characterized by having asymmetrical triangular upper molars and symmetrical or nearly symmetrical triangular lower molars without true talonids. The upper molars (Fig. 39) have a strong

external cingulum and a high main internal cusp in series with the main cusp of the premolars (cf. Simpson's figure of the last upper premolar and molars of *Peralesstes longirostris*, 1928, p. 105).

The typical symmetrodonts, including the English *Spalacotherium* and its allies, have sharply triangular upper and lower molars, but in 1925 Simpson erected a new family, the Amphidontidæ, for the reception of a very small lower jaw and a fragment of a maxilla from the Upper Jurassic of Wyoming, in which the jagged upper molar crowns were in top view widely triangular with an internal apex. The name *Amphidon* (Fig. 40), the author states (1925, p. 460, foot-

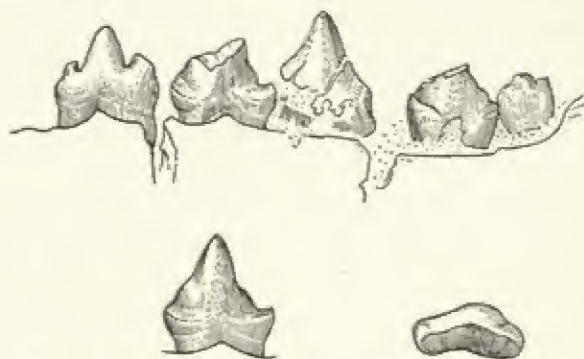


FIG. 40. *Amphidon superstes*. X10. After Simpson.

note) was given "in allusion to the anomalous character of the dentition, superficially resembling in part that of the reptilian prototype, that of the triconodonts and that of the pantotherians, in addition to its basic relationships to the *Spalacotherium-Tinodon* type." The general appearance of the lower molars indeed somewhat recalls that of the cynodonts in so far as they have a high central cusp and low incipient accessory cusps, one on the anterior and one on the posterior shearing edge of the main cusp. They also have a small anterointernal cingulum and a small posterior projection of the posterior cingulum. Seen from above, the lower molar crown forms a widely open or obtuse triangle, the apex or main cusp being toward the external or labial side.

An upper molar (Fig. 44 A), named *Eurylembda æquicrurius* by Simpson, is tentatively referred to the family Amphidontidæ but may possibly belong to the family Spalacotheriidæ. This upper molar crown when seen from above forms a very widely open triangle with the tip internal. The wide base is formed by a sharp external cingulum and there are rather well formed cusps on the anterior and posterior slopes of the main cusp. Simpson (1925, p. 469) considers that it is rather difficult to see how reduction or retrograde evolution of a well developed spalacotherid molar could produce the *Amphidon* type and he notes that, on the other hand, "*Amphidon* approaches in many respects the ancestral type which would be postulated on the theory that the accessory cusps arose in place, instead of migrating or rotating [as assumed in the Cope-Osborn theory of the origin of the tritubercular molar]. Conversely, the actual existence of such a type increases the probability that the cusps did so arise [that is, *in situ*]. No doubt," he continues, "the character of the cingulum heels in *Amphidon* is an independent specialization, but it is slight and does not alter the fact that here we have a triangular molar, essentially symmetrical with respect to a vertical transverse median plane, functionally composed of one high sharp cusp, but with a tendency to form antero- and postero-internal cusps. And just such a molar we would expect to be ancestral to the molar of the spalacotherids."

Hence, even though the symmetrodonts are regarded by Simpson as an extinct group that did not give rise to the trituberculates (pantotherians) and higher mammals, they are nevertheless of great interest as representing, so to speak, a first attempt to produce an effective shearing occlusion of the upper and lower cheek teeth by the opposition of reversed upper and lower triangles.

The Jurassic "Pre-Trituberculate" or Pantotherian Dentitions.—We have seen above that a certain group of the later mammal-like reptiles of the Upper Triassic age experimented with a type of occlusion in which the inner parts of the trans-

versely widened upper molar crowns articulated between two circularly-based lower crowns, thus initiating a vertical crushing mechanism, and that an early group of true mammals, the symmetrodonts, worked out an occlusion pattern involving reversed upper and lower triangles, thus initiating an effective shearing mechanism. It remained for the "tritubercular-tuberculo-sectorial" mammals of late Cretaceous and early Tertiary times to develop the "cutting triangles" and the "vertical crusher" principles in combination and in the highest degree of efficiency; but already in Mid-Jurassic times the swarming and diversified tiny mammals called pantotherians were trying out numerous early experiments in which now one and now the other of these principles were stressed, or both together.

Of the several families and numerous genera of the Jurassic pantotherians only one family, the Amphitheriidae, appears to stand in or near the general line of ascent toward the modern mammals. *Amphitherium* of this family, from the Upper Jurassic of England, is known only from the lower jaw (Fig. 41). Its teeth are well differentiated into incisors,

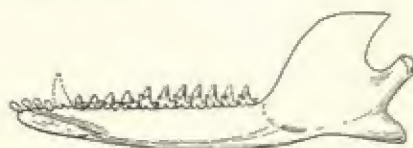


FIG. 41. Lower jaw of *Amphitherium*. $\times 2$. After Simpson.

canines, premolars and molars and the general appearance of the jaw is not unlike that of a very small opossum, except that the angular process of the mandible is not inflected and that there are seven molars on each side as opposed to four in the opossum. Also the talonids or heels of the lower molars are less extended anteroposteriorly, are not basined and bear but one cusp, corresponding to the entoconid. Unfortunately the upper molars of *Amphitherium* are not known, but Simpson observed (1928, p. 117) that in one well worn lower molar there was an oblique rounded groove in the unbasined heel,

running straight externally and downward from the notch between the talonid cusp and the metaconid. "This oblique groove," he notes, "clearly marks the path of the protocone in the last stages of the shearing and grasping bite, and has an important bearing on molar evolution which I hope to point out in more detail elsewhere." Here then is definite evidence that the protocone of the upper molar already sheared past the metaconid on to the upper surface of the talonid of the lower molar; so that this essential condition of the tuberculo-sectorial occlusal relations seen in later mammals was already established in the most primitive of the Upper Jurassic pantotherians.

In view of the great relative antiquity of *Amphitherium* and of its morphological importance in the evolution of the molar teeth of later mammals, I attempted in 1910 (p. 180) to make a hypothetical restoration of an upper molar of *Amphitherium* after comparing its lower teeth with those of the recent opossum and with those of its own approximate successors the dryolestids. The more accurate data now supplied in Simpson's memoirs prove that my conception in 1910 of the exact position of the trigonids of the lower molars of *Amphitherium* was essentially incorrect, inasmuch as I placed the axis of the protoconid-paraconid shear too much transversely and not enough anteroposteriorly. The result was that the posterior slope of my hypothetically reconstructed upper molar was also too transverse, not tilted sufficiently toward the rear. Hence the reconstruction as a whole was too short anteroposteriorly on its outer side in proportion to its transverse diameter. Using Simpson's new data as a basis, it now seems evident that, on account of the marked forward slope of the paraconid-protoconid shear, the posterior slope of the upper molar must also have been inclined in the same direction. Moreover the transverse narrowness of the trigonids does not favor the great transverse width of the entire upper molar which is seen in my earlier restoration. Since there was a sharp incision in the paraconid-protoconid blade between these two cusps and a similar incision between the

protoconid and metaconid, the probability of the presence of sharply defined proto- and metaconules in the upper molar becomes high. As the paraconid of each lower molar juts forward above the talonid of the preceding molar, the antero-posterior space left for the inner projection of the tip of the protocone is small; but since, as observed by Simpson, there was a definite groove made by the tip of the protocone in the downward and outwardly sloping floor of the talonid, we are fully justified in putting the narrow protocone in its usual position behind the metaconid. Since the talonid bears no hypoconid, the probability is slight that the amphicone was divided into distinct para- and metacones. And since in all the known upper molars of symmetrodonts and pantotherians the upper molars formed an asymmetrical triangle with a projecting overlapping parastyle, oblique ectoloph and strong external cingulum, it is very likely that the primitive *Amphitherium* already foreshadowed these characters.

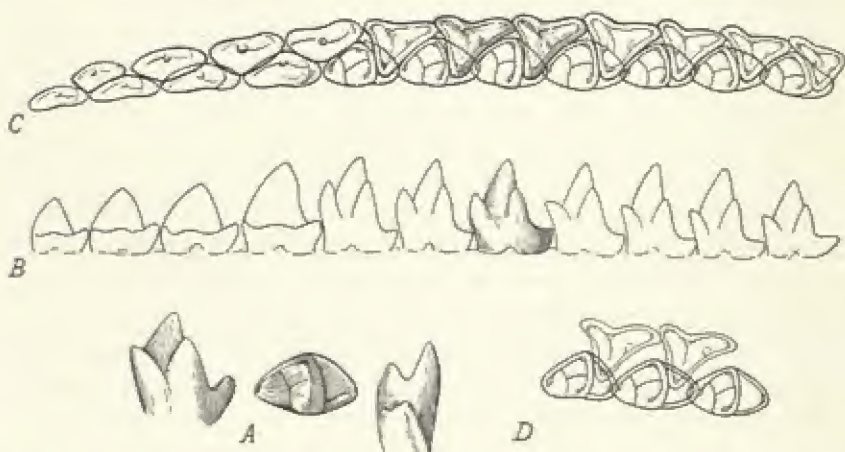


FIG. 42. Attempted restoration of the upper cheek teeth of *Amphitherium*, as inferred from facts regarding the lower dentition supplied by Simpson. Enlarged.

The resulting partly hypothetical restoration (Fig. 42) of an upper molar of *Amphitherium* reveals an extraordinarily generalized type structurally allied on the one hand to that of the symmetrodonts and on the other potentially ancestral to

the later specializations of the dryolestids and even of the Cretaceous marsupials and insectivores.

The lower premolars of *Amphitherium* as described by Simpson show a regular increase in size and a slight increase in complexity as we pass from p_1 to p_4 . All are two-rooted teeth, as are the molars and the canines. Each premolar has a sharp internal cingulum which ends posteriorly in a small projecting heel or talonid. This internal cingulum in the premolars seems to represent the paraconid, metaconid and talonid cusps of the molars; the actual origin of a paraconid from the upgrowth of the cingulum is plainly indicated in *Peraspalax* (Simpson, 1928, p. 141). The premolars are each supported by an anterior and a posterior root as in the molars. But there is nevertheless a marked morphological gap between the premolars and the molars in all known pantotheres. It is possible that this difference may be connected with the fact that the premolars of adult pantotherians belong with the replacing set, while the molars may be serially homologous with the milk teeth, which in many mammals are more molariform than the teeth which replace them. In any case it is a fact that in the higher cynodonts, in the triconodonts, symmetrodonts and pantotherians there is a rather pronounced regional anisomerism between at least the anterior premolars and the molars. In many later mammalian families, especially among the ungulates, this initial difference was gradually overcome by the progressive molarization of the premolars.

The genus *Paurodon* from the Upper Jurassic of Wyoming is regarded by Simpson as a structural derivative of *Amphitherium*. It is remarkable in that the number of its molar teeth was reduced to four, the same as in primitive marsupials. But though these molars are well spaced, they show only small talonids. The premolars are reduced to two, marking this genus as a specialized side branch.

Essential features of the basic tritubercular-tuberculo-sectorial dentition are that the upper molars are much wider transversely than the lower molars and that the trigonids of

the lower molars fit into the interdental embrasures or notches between the upper molars. These relations, though only inferential in the case of *Amphitherium*, are well established in another Jurassic pantotherian, *Amblotherium pusillum* (cf. Simpson, 1928, p. 134, Fig. 42), in which both upper and lower molars are preserved. In *Amblotherium* the upper molar crowns (Fig. 43) are dominated by a high internal cusp, the protocone, which has every appearance of being serially homologous with the tip of the last upper premolar (cf. Simpson, p. 137, Fig. 43), as shown also in the related genus *Kurtodon* (*op. cit.*, p. 141, Fig. 45).

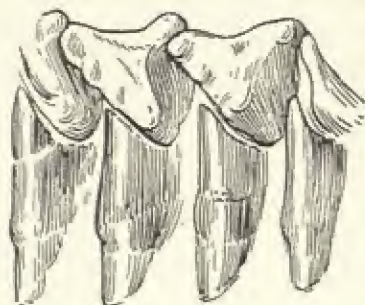


FIG. 43. *Amblotherium pusillum* (Owen). Crown view of upper molars and external view of associated lower molars. $\times 12$. After Simpson.

It was long difficult to decide whether the molar homologue of the premolar tip in the American pantotheres is the amphicone or the protocone (as maintained by Osborn). But since in either case the outer side of the upper teeth, according to much evidence, always overhangs the lower teeth, the observed occlusal relations in typical pantotherians as figured by Simpson (1929, p. 71) could have been produced if there had been an inward growth of the inner side of the upper molar crowns, causing the protocone to shift inward, and if there had been at the same time a correlated inward growth of the paraconid, metaconid and talonid cusps of the lower molars (Fig. 44).

According to the Cope-Osborn theory (Fig. 8) the relation of reversed triangles in the upper and lower molars was

produced by the rotation or folding up of a primitive triconodont type, inward in the upper jaw, outward in the lower jaw; but Simpson has greatly weakened this theory by pointing out that there is no evidence that the triconodonts gave rise to the symmetrodonts or that the latter gave rise to the pantotherians; also that the evidence supplied by *Amphidon* and other forms suggests rather that new cusps arose *in situ* and did not rotate. After thirty-odd years of recurrent struggling with this subject, I now feel that there were certain elements of truth in each of the several theories of the origin of the reversed triangles: in the Cope-Osborn theory of rotation (Fig. 8), in the premolar analogy theory of the origin of cusps *in situ* (Fig. 18), in Gidley's theory of the correlative development of the protocone of the upper molars with the talonid of the lowers, in the wedge theory of unlike upper and lower molars proposed by me in 1910, and finally in the theory of inward growth of both upper and lower molar crowns proposed by me in 1926 (Fig. 23). Each theory was supposed to exclude all previous theories but continued reflection has led me to the view that not all parts of the rival theories are mutually exclusive. For example, a protocone of a later stage lying on the lingual side of the upper molars might be and probably was once homologous with the correspondingly placed cusp of the last upper premolars, and yet it might originally have been the highest tip of the crown; so that it might be older than the talonid and yet subsequently develop with it. The inward extension of the protocone (Fig. 44) might bring about a false appearance of rotation of the paracone and metacone and yet these cusps might have arisen *in situ*, originating as an undivided amphicone on the outer slope of the protocone, and so forth.

The diagram in Fig. 44, which has grown out of several of my earlier diagrams but is now corrected from the data supplied by Simpson's memoirs, shows very clearly how by an inward growth of the inner side of the upper teeth and by a correlated inward growth of the paraconids and metaconids of the lower molars, an originally *Amphidon*-like tooth derived

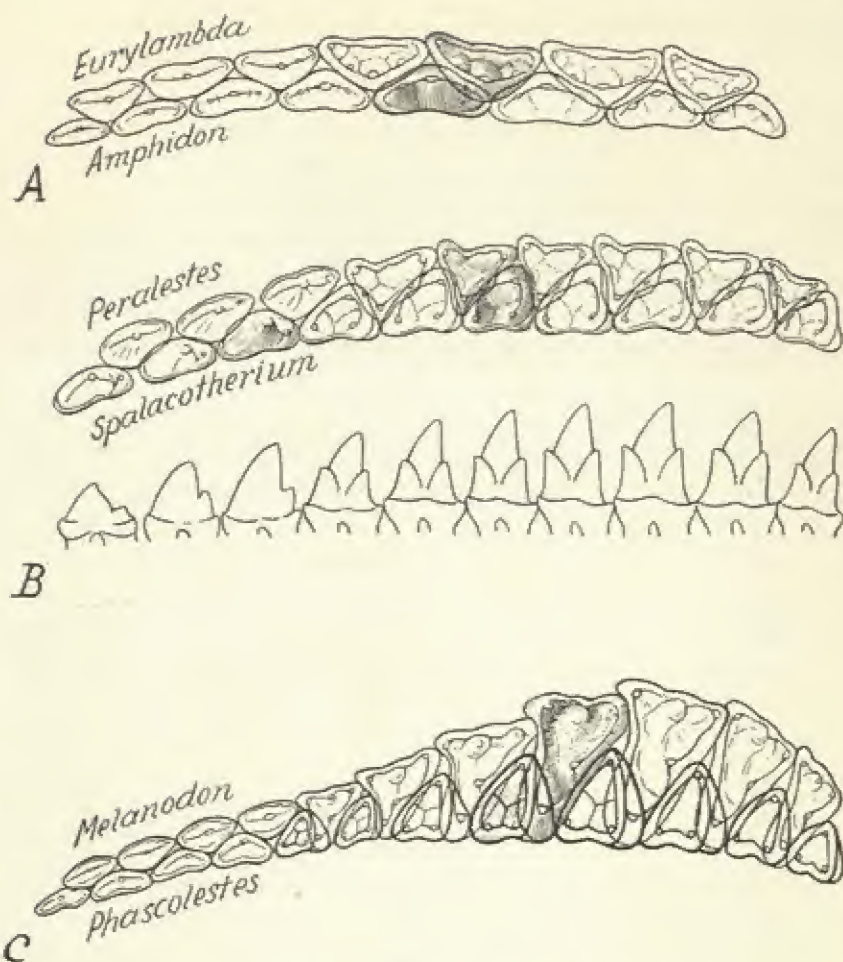


FIG. 44. Theory of progressive transverse extension of the upper molar crown, with consequent inward shift of protocone tip. Partly hypothetical restorations of upper and lower cheek teeth in occlusion, based chiefly on the facts recorded by Simpson.

- A. Stage of the primitive symmetrodont: *Amphidon* (lower), *Eurylambda* (upper).
 B. Stage of advanced symmetrodont: *Peralestes* (upper), *Spalacotherium* (lower).
 C. Stage of advanced pantotherian: *Melanodon* (upper), *Phascolestes* (lower). Scales various.

eventually from a cynodont shearing crown could give rise by a series of easily understandable steps to the occlusal pattern seen in the wide-toothed pantotherians. Such pro-

gressive transverse extension, of which we have the most convincing evidence both in pantotherians and in later mammals, would produce the appearance of reversed triangles which Cope and Osborn perceived as essential. Moreover, the theory of correlated transverse inward extension of both upper and lower molars in the ancestors of the pantotherians accounts for *all* the occlusal relations of the upper and lower molars by a single principle: from it we understand, for example, why the protocone in *Melanodon* (Fig. 45 H), *Malthacolestes* (Fig. 45 C), etc., forms a V-shaped cusp with

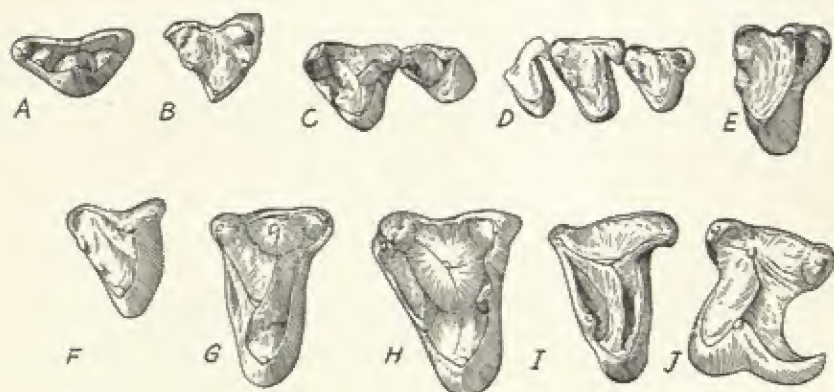


FIG. 45. Theory of progressive transverse extension of the upper molar crown in Jurassic symmetrodonts (A, B) and pantotherians, based on facts deduced from Simpson's text and illustrations. A. *Eurylambda aequicrurius*. B. *Peralestes*. C. *Malthacolestes*. D. *Pelicopsis*. E. *Eutlaster*. F. *Amblottherium*. G. *Herpetairus*. H. *Melanodon oweni*. I. *Melanodon goodrichi*. J. *Docodon*. Scales various.

a transverse ridge connecting the protocone with the amphicone (because its tip has grown inward and the transverse ridges mark the direction of its extension), why the metaconule of *Herpetairus* (Fig. 45 G) and allied genera should also be V-shaped, since it has shared in the inward extension of the crown; we also begin to see how the amphicone arose *in situ* by budding off from the lingual face of the high cingulum (Fig. 45 C, E, F); how in the lower molars the paraconid and metaconid are produced inward since they shear past the inwardly-produced ridges of the protocones (Fig. 44); even the incipient talonid of *Amphitherium* (Fig. 42 A) seems to

have arisen as an indirect response to the presence of the inwardly-grown protocone (Fig. 42 B); for in this genus, as Simpson has shown in an old specimen, the shearing pressure of the talonid against the tip of the protocone produced a rounded groove running straight externally and downward from the notch between the talonid cusp and the metaconid (Fig. 42 A).

From the central Jurassic pantotherians such as *Amphitherium* sprang the insectivore-like family of the Dryolestidæ (Fig. 46), with very high sharp-pointed trigonids and very



FIG. 46. Lower molar of American Jurassic dryolestid, *Phascolestes*. $\times 10$. After Simpson.

short talonids. Perhaps from the Dryolestidæ branched the strange Docodontidæ, in which the primitive tuberculo-sectorial character of the lower molars was submerged in the massive cusps and crests, together with an expansion of the talonid basin correlated with a huge expansion of the protocone or internal cusp of the upper molars (Fig. 45 J). There is every reason to believe, however, that neither of the extremes represented respectively by the dryolestids and the docodonts gave rise to the line or lines leading to the marsupials and placentals of the Tertiary period but that these forms sprang from the more central pantotherian stock represented by *Amphitherium*.

The Upper Cretaceous Marsupials and Insectivores.—Scores of millions of years passed between the time of the Upper Jurassic pantotherians of England and Wyoming and the first recorded appearance of true marsupials and placentals in the later part of the long Cretaceous period. By that time these two subclasses of mammals had already become widely separated. We do not know the exact source of either but each had carried much further some of the peculiarities that

were already initiated in the molar teeth of different families of pantotherians. The Upper Cretaceous marsupials, found as contemporaries of the giant dinosaurs of Montana and Alberta, were members of the same family as the modern opossum; one of them, named *Eodelphis* by Dr. W. D. Matthew (Fig. 47), was almost indistinguishable from the

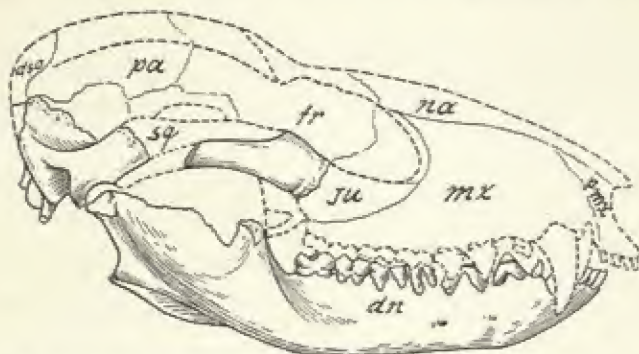


FIG. 47. A primitive opossum from the Upper Cretaceous of Alberta, *Eodelphis brotoni*. Natural size. Reconstructed mostly from data by Matthew.

opossum *Didelphis* in its lower jaw and such parts of the skull as were preserved.

The scattered upper molars of these Upper Cretaceous marsupials described long ago by Marsh and by Osborn under the names *Pedimys*, *Protolambda*, etc., are notable for the presence of one or several cusps near the outer cingular border of the tooth, which are collectively homologous with the external cingulum cusps (Fig. 48). Winge (1882) took these cusps to be the original elements of the mammalian molar crown and based an elaborate system of nomenclature upon this assumption; but if the protocone of the pantotherian upper molars represents the original tip of the crown, then the protocone or main inner cusp of the Upper Cretaceous didelphids probably does also. In these upper molars we witness an early stage in the tendency toward anteroposterior lengthening of the outer part of the crown, which tendency was correlated with a marked increase in size of the talonid, together with an insinking or basining of its dorsal surface

so as to embrace completely the surface of the large protocone of the upper molar.

The opossum had already been selected by Huxley, Dollo and Bensley as the living embodiment of the skeletal characters that one might expect to find in the remote common ancestors of the highly diversified fossil and recent marsupials of North America, South America, Europe and Australia. Therefore it is reassuring to find such relatively very ancient

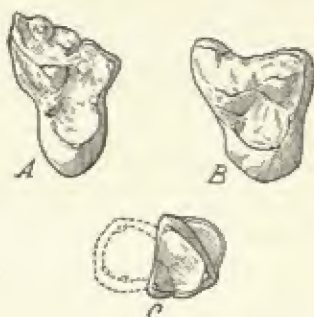


FIG. 48. Teeth of Upper Cretaceous marsupials.

- A. Upper molar of *Pediomys* sp. $\times 6$. After Simpson.
 B. Upper molar of *Pediomys* sp. $\times 3$. After Simpson.
 C. Lower molar. After Osborn. Circa 6/1.

fossil forms as *Eodelphis* in the Upper Cretaceous, which fully establishes the antiquity of the opossum family. When we seek among the Jurassic mammals for still more remote ancestors of the opossums, we find that each one of several groups suggests the opossums in certain features but differs in others. In the triconodonts, for example, the skull and braincase were rather opossum-like but the jaw differed in certain important characters and the dentition was widely different. The opossums might be derived from *Amphitherium* (Fig. 41) by the inflection of the mandibular angle, the reduction of the number of lower molars from seven to four, the development of the talonid and of an anteroexternal cingulum on the lower molars, etc. But we have no evidence that *Amphitherium* was the real source.

Similarly we might see in the numerous and often massive external cingulum cusps on the upper molars of the Upper Cretaceous opossums a possible derivative from the strong outer cusps of such a symmetrodont as *Peralesstes* (Fig. 39). But while we may never, through lack of specimens, be able to tell exactly which Jurassic form did give rise to the opossums, we can at least see that the opossums have travelled much farther along the road of dental evolution than did any of the Jurassic pantotherians except the dicrocynodonts, which were a very aberrant family. For in the opossums we have an early stage of a tendency toward secondary antero-posterior growth of the upper and lower molars which is carried much further in many of their modern relatives, especially the herbivorous diprotodonts. In the lower molars this anteroposterior growth was manifested in the greatly increased size of the talonid and in the upper molars in the division of the amphicone into two well separated cusps, the para- and metacones. In the modern opossums (Fig. 49) we



FIG. 49. Upper and lower cheek teeth of a modern opossum (*Didelphis virginiana*).
X $\frac{3}{2}$.

have a secondary emphasis of the metacones and a secondary reduction of the paracones.

One thing at least is highly probable: that although the primitive marsupials may be said to have tuberculo-sectorial molars and the primitive Eocene placentals also had tuberculo-sectorial molars, yet the two sets of molars differed in many details and may very well have been derived independently

not from a strictly common origin but from the diverse molars of different families of Jurassic pantotherians.

The Upper Cretaceous Placentals.—These forms are best known from half a dozen imperfectly preserved, very small skulls discovered by Doctor Granger in the Gobi Desert, one of the most important palæontological prizes of Dr. Roy C.

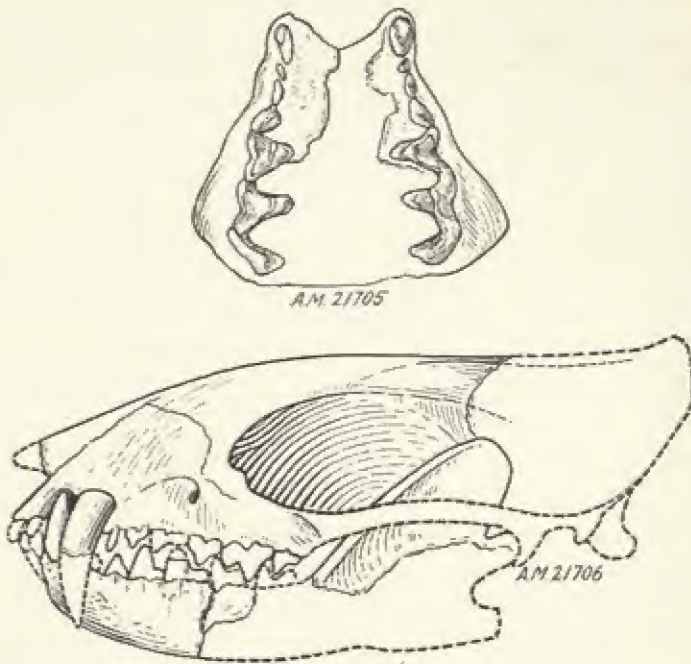


FIG. 50. An Upper Cretaceous insectivore from Mongolia, *Deltatheridium pretrituberculare*.

Upper figure: palate and cheek teeth. $\times 2/1$.

Lower figure: skull restored. $\times 2/1$.

After Gregory and Simpson.

Andrews' explorations in Mongolia. In these small forms, described by Gregory and Simpson in 1926, the dentitions although already diversified into various generic types were almost precisely what would have been expected in remote common insectivorous ancestors of all the higher or placental orders of mammals. For one group of these little forms, the family Deltatheridiidæ, present an ideal archetype (Fig. 50)

for the divergent dentitions of the later zalambdodont insectivores and early Tertiary and later carnivores. In another family, the Zalambdalestidae, the molars seem to be tending toward the leptictid and hedgehog (erinaceid) types.

Some of these Upper Cretaceous placentals contrast widely with the contemporary opossum-like marsupials in that the upper molars lack the massive external cingulum cusps and have the para- and metacones nearer to the outer border of the crown (Fig. 51). The two last named cusps

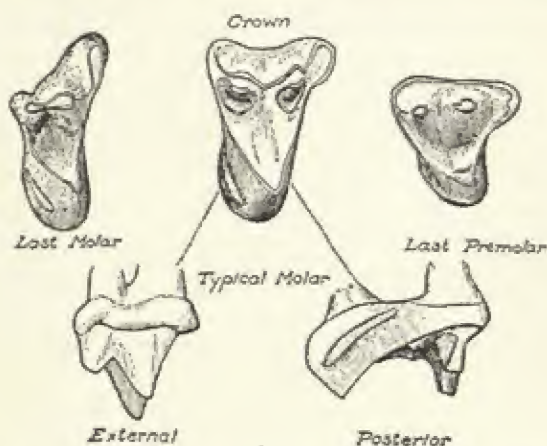


FIG. 51. An Upper Cretaceous insectivore from North America, *Gyponictops hypacodus*. Upper cheek teeth. $\times 8$. After Simpson.

are barely separated in *Deltatheridium* but are well separated in *Zalambdalestes* and *Gyponictops*, the latter (Fig. 51) approaching the upper molar pattern of certain Eocene insectivores of the family Leptictidae (Simpson).

Huxley, Osborn and later writers had long regarded the Order Insectivora as standing very near to the base of the common stem of the later placental orders, so it is again reassuring to find these Mongolian Upper Cretaceous forms fitting into the expected picture of the evolution of the mammals. In the *Deltatheridiidae* the molars have advanced well beyond the Upper Jurassic stage in that the amphicone is plainly splitting into the para- and metacones, while the

talonids have grown backward so that the lower trigonids are well spaced, giving room for the protocones of the upper molars to overlap fully on to the talonids. The latter, however, are not basined but consist of straight backwardly extended projections or heels.

From the relations of the upper premolar cusps to those of the molars, the amphicones (para- and metacones) have every appearance of being in series with the tips of the premolars, while the protocones appear to represent inwardly grown buds from the base of the crown like those of the premolars of many Eocene mammals. An alternative theory to this would be that the protocones had grown far inward and then become reduced, meanwhile dragging the amphicones partly inward so as to bring them in line with the undisturbed premolar tips; but for such a theory the only known evidence is that the protocone of *Deltatheridium* has the appearance of being homologous with the protocone of the pantotherians, which in turn seems to be in series with the tips of the premolars.

Thus in spite of what I have previously written to the contrary, it is now conceivable that Professor Osborn was right both in identifying the protocone of the pantotherians with the protocone of the later mammals and in homologizing it also with the tip of the premolars. Nevertheless such a theory involves a serious difficulty, which I pointed out in 1922, namely that in all later tritubercular-tuberculo-sectorial dentitions, according to the Osborn-Cope nomenclature, the "protocone" of the upper cheek teeth shifts from the outer to the inner cusp as we pass from p^4 to m^1 , whereas the corresponding protoconid of the lower teeth remains on the outer side of the teeth both in the premolars and the molars, and that a study of the occlusal diagrams of the early Eocene mammals does not support the Cope-Osborn identification of the protocone, since it gives no evidence of such a shift either in the upper protocones or in the lower protoconids.

The difficulty may perhaps be met by the suggestion that the amphicone arose as a small cusp on the outer slope of the

protocone (Fig. 45 A), much as the para- and metaconids arose on the inner slopes of the protoconid, and that the undivided premolar tip partakes of the nature of both a protocone and an amphicone, just as the undivided protoconid of the lower molars includes the future metaconid. According to this hypothesis, the inner ledge of the upper premolar protocone, which ledge eventually plays the rôle of a protocone, is really not a protocone but a new cusp, the deuterocone, first named by Professor Scott.

In conclusion, the Upper Cretaceous marsupials and placentals show that in both these subclasses of the Mammalia the tritubercular-tuberculo-sectorial type of occlusion had been fully attained, although possibly by somewhat different routes. Here undoubtedly are the real ground-plans for the divergent evolution of the dentitions of Eocene and later marsupials and placentals.

It will also be observed that regional anisomerism in the dentition, inherited perhaps from very distant cynodont ancestors, persisted in both marsupials and placentals of Upper Cretaceous age, inasmuch as there is a rather sharp contrast between the premolars and the molars. It was not until Eocene times that in some lines the premolars began to become molarized so as eventually to replace this stage of regional anisomerism by a high degree of secondary polyisomerism.

The advent of the peculiar constriction of the opposite tooth rows behind the canines, accompanied often by a diastema between the canines and the premolars, was probably correlated in part with the evolution of the facial musculature in the early mammals. The reptiles have no orbicularis orbis and buccinator muscles, these muscles having spread forward in the early mammals from the primitive sphincter colli of the neck (Ruge, E. Huber). In the ungulates and rodents the buccinators form prominent tubes or pockets, which press in upon the toothless space behind the canines. Initial stages of this development may be seen even in the insectivore *Erinaceus* (see the figures by Boas and Paulli). The labial

muscles exert constant pressure on the plastic germs of the incisors and canines and have probably influenced the inclination of these teeth as well as the smooth shapes of their labial surfaces.

Specialized Mammalian Dentitions.—The literature of palæontology abounds in many adjectival terms designating the various types of molar tooth crowns that occur among the swarming mammals of present and past epochs. But if we tried to classify dentitions as a whole according to a natural system, the nomenclature would be more complicated than the dental formula and we should have to use a single term for each of hundreds of types. The simplest way to classify dentitions naturally is to group them according to the orders and suborders of mammals. In the present section I shall try to outline the palæontological and comparative anatomical evidence concerning the origin of the most aberrant types of dentition, with frequent reference to the phenomena of polyisomerism and its opposite. By *aberrant* types of dentition I mean such types as lie furthest from the direct line of ascent toward man and are excluded therefrom by marked specializations that have apparently been irreversible.

Multituberculates.—*Facile principes* among the most aberrantly specialized are the dentitions of the Multituberculata, a group of mammals with an extraordinarily long geologic life-span, since they appear in the Upper Triassic and last through the many millions of years of the Jurassic, Cretaceous and basal Eocene (Paleocene). They have recently been monographed by Dr. G. G. Simpson (1928, 1929), who has contributed greatly to clearing up the confusions of the older literature. *Tritylodon longævus* Owen, the most primitive of the multituberculates, from the Rhætic (Upper Triassic) of South Africa, foreshadows or suggests the rodent type in that there is a pair of enlarged upper incisors, followed by a long diastema, with two parallel rows of subcircular molars; each of these bears three rows of cusps arranged longitudinally. Thus the dentition as a whole shows a strong regional anisomerism but in the cheek teeth there is a marked intradental

polyisomerism because there are no less than three rows of closely similar cusps on each of the five upper molars.

As to the derivation of this early specialized phytivorous dentition, there can now be no valid doubt that *Tritylodon* is a descendant of some of the higher mammal-like reptiles, since, as Broom and Simpson have shown, the form and contacts of every one of the bones of the skull indicate this derivation.

In the other direction, Simpson has shown that it is by no means certain that the African *Tritylodon* and its European relatives "*Triglyphus*" and *Stereognathus* are related to the true multituberculates or Jurassic and later Plagiaulacoidea, which have enlarged grooved premolars.

The more advanced suborder of the multituberculates includes the Jurassic *Plagiaulax*, which is highly specialized in its peculiar but in some respects rodent-like dentition. In the mandible one pair of lower incisors is enormously enlarged and pointed, forming a powerful nipping organ, probably for the piercing of tough rinds and shells of seeds. As a result of the great enlargement of the incisors there is a diastema and the canine is lacking. The posterior premolar (p 4) is likewise greatly enlarged, with a very high compressed cutting edge and numerous (5-8) grooves and ridges running obliquely forward and downward on both inner and outer surfaces, the character to which the name *Plagiaulax* (oblique groove) refers. The two or three premolars immediately in front of this huge tooth are crowded and tilted forward but partake in varying degrees of its grooved character. Nothing exactly like this is known even among the diprotodont marsupials, which likewise develop grooved posterior premolars, especially the Pleistocene kangaroo *Burramys*. The function is apparently the slicing of tough rinds and nut shells, as suggested by Gidley. The lower molars are small, with a central depression or groove margined by low cusps. In the upper teeth (named *Bolodon*) the median upper incisor is procumbent and somewhat but not excessively enlarged, the premolars bear several low tubercles but the molars are greatly elongated and provided with numerous small cusps

arranged in two anteroposterior series separated by a sharp longitudinal groove. The enlargement and multiplication of oblique grooves of the secant lower premolar culminate in *Ptilodus* of the Paleocene. In another Paleocene type (*Polymastodon*) the grooved premolar has become greatly reduced and the habitus has become more rodent-like; the cusps of the upper molars multiply as the internal cingulum grows up into a third longitudinal row of cusps. Thus the plagiaulacoids represent extreme regional anisomerism with marked intradental polyisomerism in the enlarged grooved premolars and in the multituberculate molars.

As to their relationships, the oldest multituberculates are as old as the higher mammal-like reptiles and older than the known triconodonts, symmetrodonts and trituberculates; hence they can not be derived from any of the known genera of these orders. The skulls of the later multituberculates (*Ptilodus*, *Polymastodon*) present a number of curious resemblances on the one hand to the monotremes and on the other hand to the diprotodont marsupials, but there are grave objections to the derivation of either or both these groups from the multituberculates. Dr. G. G. Simpson (1928, pp. 163-171) has indeed made out a very strong case for regarding the Multituberculata as a widely distinct subclass (Allotheria) of mammals, derived independently of other Mesozoic orders and positively not ancestral to the diprotodont marsupials or to the rodents, to which they show strong convergent resemblances.

In a recent work embodying a new theory of the origin and evolution of mammalian dentitions, Dr. Friant, ignoring completely however all this mass of evidence so carefully analyzed by Simpson, selects (1933, p. 29) the tritylodontoid upper molar of the Upper Triassic "*Triglyphus*" (*Tritylodon*) *fraasi* as the starting-point for her theory of the evolution of the cheek teeth of mammals. The later plagiaulacoids of the Upper Cretaceous Paleocene and lowest true Eocene undergo certain remarkable specializations. In *Ptilodus* and its relatives the upper molars acquire three longitudinal rows

of small cusps, but Simpson has shown (1928, p. 47) that as the second upper molar is decidedly nearer to the midline than the tooth in front of it, the new row of cusps grows up on the inner side of the first molar and on the outer side of the tooth behind it, so as to permit the anteroposterior movement of the lower teeth along two longitudinal grooves extending over m^1 and m^2 . Meanwhile the two rows of cusps on the crown of the lower molars become subequal in height. No better example could be found of the intimate mechanical correlation of the upper and lower teeth in phylogeny. And if Mlle. Friant had not disregarded Doctor Simpson's work on the Mesozoic mammals she might perhaps have cited this instance in support of her view that correlated changes in the upper and lower teeth take place as a result of movements of the mandible in the foetal stage during the plastic condition of the tooth germs. In the line leading to *Polymastodon* the great grooved lower premolar lost its functional value and became reduced to a peg-like tooth with a few feeble grooves.

Monotremes.—The modern monotremes of the Australian region retain in their reproductive systems as well as in certain features of their skulls, pectoral and pelvic girdles and limbs the most direct evidence of their ultimate derivation from the higher mammal-like reptiles. In their dentitions, however, they are much specialized in different ways. *Echidna* and *Proechidna* have lost all teeth and converge toward certain edentates in their ant-eating adaptations. In *Ornithorhynchus*, however, minute true cheek teeth are found in very young skulls but are later cast out, their places being taken by horny plates developed in the gum. These transitory teeth of *Ornithorhynchus*, long ago described by Poulton, have been studied by various authors, of whom the latest is Dr. G. G. Simpson (1929). In many features they are so utterly different from the teeth of all other known types of mammals that it is impossible to identify their cusps with any assurance. Each of the two upper molars is extended longitudinally and subdivided into anterior and posterior moieties separated by a deep median notch on the lingual border. Each moiety

consists of a high, more or less V-shaped inner cusp with one or two cross crests running toward the irregular multicuspidate outer border. The lower molars have a somewhat similar but reversed pattern. To the present writer the excellent figures and occlusion diagram published by Simpson suggest the derivation of these patterns by extreme degeneration from a somewhat *Cænolestes*-like stage, with elongate molars and sharp emphasis of the proto- and hypocones. On the other hand, Doctor Simpson (1929, p. 9) has stated a number of serious objections to all such proposed derivations from normal tuberculo-sectorial dentitions. Nevertheless a reëxamination of three very young skulls of *Ornithorhynchus* that were kindly supplied by Mr. Harry Burrell, the noted Australian authority on that animal, has suggested a quite different yet possible theory of the derivation of the curious monotreme molars. In my 1910 book on the *Orders of Mammals* I pointed out that embryological evidence discovered by Broom and others suggested that at no very distant date the diprotodont marsupials, like the monotremes, laid eggs and like them had a reptilian type of pectoral girdle in which the large coracoids extended inward to meet the sternum. There are so many deep-seated mammalian characters of the brain, hairs, milk glands, etc., of monotremes that a separate derivation from Triassic reptiles is very difficult to accept. My tentative hypothesis is, therefore, that the *Ornithorhynchus* is an excessively specialized derivative from the Australian phalangeroid stem, that its "beak" represents an enormously hypertrophied rhinarium of the type seen in *Phascolarctos* and that the two V's of its upper molars correspond with those of *Phascolomys*; also that the "reptilian" characters of its reproductive organs have arisen from a neotenuous arrest of ontogenetic phases that are transient in the diprotodonts; that excessive aquatic adaptation accounts for many of the other specializations of the skeleton. The existence of *Echidna* (= *Tachyglossus*) and its even more specialized relative *Proechidna* offers no difficulty at all to this view, since these forms are obviously derivable

from an *Ornithorhynchus*-like ancestor after the assumption of land-living habits and of edentulous specializations of the jaws and skull.

The transitory teeth of *Ornithorhynchus* were described as "multituberculate" by Cope, but Osborn (1907, p. 107) showed that they differed fundamentally from the multituberculate type, while Simpson, after the most penetrating and comprehensive analysis, proved that these peculiar teeth are widely different not only from the multituberculate type but also from the varied types of Mesozoic triconodonts, symmetrodonts, and pantotherians. He also says (1929, p. 14): "A vague resemblance to the triconodonts may eventually prove to be significant but at present is not trustworthy. The evidence, not wholly negative, thus tends to emphasize the sharp separation from all other mammals seen throughout the whole organization of *Ornithorhynchus*. . . ." He suggests, however, a possible way in which such teeth could be derived by "primary longitudinal differentiation into two main cusps, and transverse differentiation through the upgrowth of cingula, as suggested in *Diademodon* or *Pachygeneleus*, on opposite sides of upper and lower teeth." In recognizing the processes of longitudinal differentiation and transverse differentiation Doctor Simpson comes close to the phenomena here called respectively anteroposterior and transverse polyisomerism.

Several other groups of mammals apparently quite independently developed what Doctor Simpson has well called the "Plagiaulacoid" type of mammalian dentition (1933, pp. 97-107). In this very intensive analysis as well as in his "Affinities of the Polydolopidæ" (1928) he deals most effectively with the long-lived error that the multituberculates gave rise to the fossil polydolopids and cænolestids of Patagonia, or to any of the modern diprotodont marsupials with grooved secant premolars, or to certain Eocene tarsioids (*Carpolestes*), all of which possess in their dentitions the main adaptive features of the typical multituberculates.

Diprotodont Marsupials.—As to the derivation of the varied dentitions of the diprotodont marsupials, Bensley's admirable analysis holds good after thirty years, but is regularly disregarded by the proponents of new theories. The lower front teeth becoming procumbent and rodent-like, as has happened independently many times in different groups, a diastema develops, the canines become reduced and the posterior premolars become grooved. The upper molars in the more primitive phalangers consist of two pairs of widely open V's. Emphasis of the cross-crests produces the bilophodont molars of the kangaroos and finally those of the family Diprotodontidæ, which paralleled the proboscidean *Dinotherium* in the shape of the cheek teeth. In another direction the great emphasis of the compressed secant premolars produces the lion-like *Thalacoleo*, a specialized phalangeroid.

In the wombats the crowns of the molars became excessively heightened and curved transversely, paralleling those of rodents, while the strong paired incisors, both upper and lower, complete the convergence toward the rodents. In each and every diprotodont we see the struggle of the forces of anisomerism and polyisomerism, the latter producing resemblances not only between the molars of the same species but also between those of widely separated genera. But in every case there is strong evidence against derivation of the diprotodonts from the multituberculates.

Placental Rodents.—We may also and with even greater positiveness exclude the multituberculates from the ancestry of the placental rodents; first, because the known multituberculate skulls abound in strange specializations, such as the reduction of the jugal, the forward lateral projection of the parietal, etc., which are unknown in the skulls of rodents; second, because the rodents resemble the multituberculates only in those general habitus features which have again and again been acquired independently; third, because the oldest rodents of the Eocene family Ischyromyidæ are the least like the multituberculates. In 1910 Dr. W. D.

Matthew published a beautifully illustrated article in the Bulletin of the American Museum of Natural History in which he showed that the oldest known rodents from the Lower Eocene of North America had skulls and dentitions of very primitive character which have been largely preserved in the existing squirrels and marmots, and that the rodents of Upper Eocene and Oligocene times clearly pointed the way toward the long-crowned molars with folded enamel crests of the beavers, geomyids and hystricomorphs. In the more primitive murids also the molars have low cusps and are not yet heightened into the zig-zag plates of the voles. Forsyth Major (1893), starting with the modern squirrels, concluded that "in the most brachyodont and therefore most primitive molars" the crowns were "polybunous"; also that in the primitive molars of placentals the cusps were arranged in longitudinal rows, three rows with two intermediate grooves in the upper teeth and two rows with one intermediate groove in the lower teeth. While citing the multituberculates as a stumbling-block to the theory of trituberculy, he neglected to point out that the multituberculates themselves assuredly do represent a very distinct phylum which is definitely excluded from ancestry to any placental orders by numerous specializations of the skull and dentition. He was also unaware (at least at the time) of the far more primitive ischyromyid rodents in the Lower Eocene of North America, whose molars were still less like the multituberculate type.

It is in vain therefore that Doctor Friant tries to derive such highly specialized rodent molars as those of *Geomys* and *Hystrix* from the six-cusped "*Triglyphus*" type, for even within the Sciuromorpha, as Schlosser (1890) long ago pointed out, there are many intermediate stages between the almost tritubercular molars of the more primitive squirrels and the folded molars of *Castor*. That the still more primitive molars of the Eocene *Paramys* (Fig. 52 A) and *Ischyromys* were derived from a typical tuberculo-sectorial type is indicated by the fact that the protocones of their upper molars fitted squarely into the talonids of their lower molars, and

that the hypoconid of their lower molars fitted between and lingual to the para- and metacones of the upper molar, as they still do in existing squirrels.

Since these lines were written I have read the paper of Dr. Serge Frechkop of Brussels (1932) in which he traces (IX,

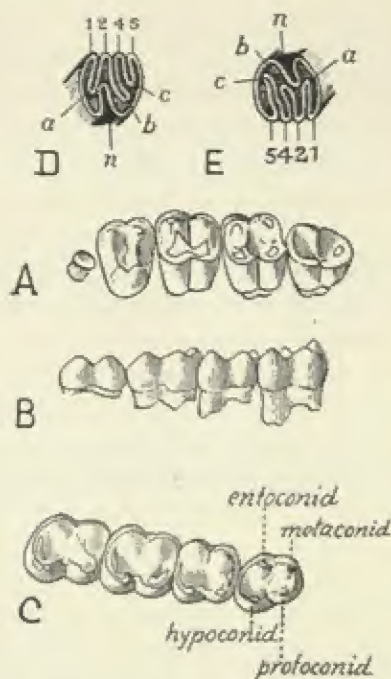


FIG. 32. Check teeth of rodents. Scales various.

- A. Left upper cheek teeth of *Ischyromys typus*, Oligocene, North America. After Matthew.
 B, C. Right lower cheek teeth of *Paramys robustus*. Middle Eocene, Wyoming. After Matthew.
 D. Left upper first molar, and E, Right lower first molar of beaver (*Castor fiber*). After Frechkop.

p. 14) with the greatest clearness the evolution of the more complex forms of sciuriform molars from the essentially tritubercular type of *Sciurus* in divergent directions toward the folded and lophodont crowns of *Anomalurus* and *Sciuropterus*. In a footnote (XII, p. 3) he says: "Bien que M^{lle} Friant insiste sur le fait que les Rongeurs, 'en dépit de

la grande diversité de leurs dentitions, n'ont aucun représentant ni fossile ni actuel à molaire trituberculée,' la trituberculie initiale nous paraît être à peine dissimulée par le développement des *cingula* dans les molaires des *Sciuridæ* (cf. notre note IX, fig. 1), où la nature secondaire de l'*hypocone*, issu du *cingulum* postérieur semble bien évidente." From reading Mlle. Friant's text one gets the impression that if she ever heard of *Ischyromys*, she has failed to appreciate its significance for her theory.

The forces of inter- and intradental polyisomerism, continuing along divergent and convergent routes since perhaps Paleocene times, have left a vast and tangled mass of documents for the confusion of odontologists, who for the most part avoid all difficulties by looking only at a few types that happen to be at hand. It is therefore a real pleasure and relief to turn to Doctor Frechkop's masterly analyses of the evolution of rodent molars from the tritubercular stem form.

In some of the unworn rodent teeth figured by Friant the folds sometimes end above in rounded cusps, recalling those of the molar plates of the elephants. Doctor Friant therefore speaks freely of the relationship between the Proboscidea and the rodents, apparently overlooking the significance of the fact that the oldest and most primitive proboscideans, *Moeritherium* and *Palæomastodon*, are also the least like the rodents, with high plated molars. Although the rodents have elongated glenoid fossæ and ovoid mandibular condyles, the movements of the jaw in the more primitive forms are not symmetrically anteroposterior but obliquely transverse. Thus the primitive rodent differed widely from the typical multituberculate, in which anteroposterior ("mesiodistal") movements of the mandible were predominant.

Doctor Friant (1933, p. 113) assumes as her starting-point a mandible which can move freely and equally in all directions in the horizontal plane; such movements would, she believes, favor the arrangement of a great number of points of calcification, all similar in form and equal in importance. Such is her ideal archetype, figured on our page 275, with two antero-

posterior rows of three equal cusps. This would be the sort of solution proposed by a mathematician to whom one hypothesis is as good as another; but the palæontologist asks, not is such a thing conceivable, but did it happen? And here the evidence from all sides is overwhelmingly against Mlle. Friant's solution. For not even the multituberculates ever realized her conditions of equal movements of the mandible in all directions, while all the known Mesozoic triconodonts, symmetrodonts, pantotherians and the known insectivores, creodonts, protoungulates and primates and even the primitive rodents adopted solutions involving the prevalence of vertical over horizontal components in the excursions of the mandible.

Lagomorphs.—The hares and rabbits were removed to a separate order, the Lagomorpha, by Gidley in 1912 and there is no doubt that the Lower Oligocene representatives of the group (*Palæolagus*) were already sharply separated from all other rodents. The distinctive feature of the lagomorph molars, as shown by Forsyth Major, is the invasion of a deep notch from the lingual side which divides the crown into two appressed tall flat columns. But, although Forsyth Major was an opponent of the theory of trituberculy, he showed that the notch was a later acquisition and that the unworn surfaces of the molars presented a pattern of cusps and grooves which he suggested might well be derived from the *Plesiadapis* type, an almost typical "tritubercular" pattern. Osborn (1907) therefore reckoned the lagomorphs as among those specialized groups in which there was a reasonable evidence of derivation of the molar patterns from the tritubercular type. Polyisomerism, both interdental and intradental, is marked in all the molars and in the posterior premolars.

The study of the evolution of the molar teeth of rodents emphasizes the principle that both inter- and intradental polyisomerism are due to budding or repetition of parts that behave as units. But the quite unsolved problem is, how do these parts, which were originally mere parts of other parts,

achieve sufficient unity and coherence to behave as units? Or to put it the other way around, what causes the forces of growth to limit themselves and concentrate at certain points of the dental lamina, so that folds which are at first barely detectable often become extremely conspicuous in later generations, like the secondary, tertiary and quaternary folds of the septa in nautiloids? In both cases it would seem that progressive hereditary factors are predominant. Folding is doubtless due to unchecked proliferation within, bounded by a limiting medium without. If the limiting medium is very strong the folds may be deflected from their primitive direction or may be crumpled into secondary folds. Notches and embrasures mark the site of sharp arrests of growth, or nodal points of relative stability on either side of rapidly growing parts. Changes in pattern then are doubtless conditioned by changes in the intensity and duration of growth of the several parts; the same may be said of changes in skull contour or in the proportions of the limbs.

In rodents with highly folded molars one of the most curious and significant features is that not only are the left and right crown patterns of the upper jaw or lower jaw respectively mirror images of each other, but the pattern of a given lower molar is also reversed in the anteroposterior direction compared with that of the opposite upper (Fig. 52 D, E). That is, the anterior end of a lower molar is homodynamous with the posterior end of an opposite upper, and the reverse. This fact has been abundantly established by such careful observers as Forsyth Major, Hinton (1926, p. 105) and Frechkop, especially in the highly specialized hystricomorphs and voles. Frechkop's figures illustrating the known stages in the evolution of the folded molars of the Sciuridæ, Anomaluridæ and myxoids show that this inverted homodynamism of the upper and lower molars is reached by convergence in the different families, starting from a tuberculo-sectorial stage or from its later derivatives. It is probably associated with increased ability of the mandible to move backward as well as forward, inward as well as outward. In

this curious phenomenon heredity and ontogeny seem to be intricately combined.

Edentates.—This is another group which contains certain families that achieve a high degree of specialization in the form of columnar and infolded crowns in association with herbivorous diet. In Professor Osborn's "Evolution of the Mammalian Molar Teeth" (1907) he pointed out that the molars of *Conoryctes*, one of the more ancient "ganodonts," as they were then called, plainly approach the tuberculo-sectorial type, but the steps connecting the edentate molar patterns with those of more primitive mammals are not yet known.

Mlle. Friant rightly considers the multiplication and simplicity of the columnar teeth of the giant armadillo *Priodontes giganteus* to be a secondary condition. It is indeed a capital example of secondary polyisomerism derived from the more primitive regional anisomerism illustrated in the palæanodonts. Such polyisomerism often precedes the complete loss of teeth, as observed in the anteaters (*Myrmecophagidæ*) and, quite independently, in the scaly anteaters (*Manidæ*).

Tubulidentates.—*Orycteropus* represents a totally different order, marked by excessive multiplication of small tubular columns in each molar. Jepson (1932) has recently described a form from the Lower Eocene of Wyoming which foreshadowed the tubulidentates in many features. In any event the group is marked by high intradental polyisomerism of the dental columns. Its skull and other skeletal characters indicate that it is a highly specialized descendant of some unidentified late Mesozoic placental stock.

Ungulates.—The multitudinous molar types in the various ungulate groups have very probably been derived ultimately from the tritubercular type, as abundantly shown in numerous works by Osborn and others. Nevertheless I am here classing all ungulates as "aberrant" simply for the reason that none of them could or did give rise to the line that led toward man, who in the eyes of anatomists and odontologists is still the central figure of the animal world. In view of the well known

review of the divergent evolution of the molars of ungulates that is to be found in Professor Osborn's "Evolution of the Mammalian Molar Teeth," it seems unnecessary here to do more than to refer to certain features bearing on our central theme of polyisomerism and its opposite.

The old error of Cope that *Phenacodus* was the "five-toed atavus of the horse" still persists in spite of the fact that it has been repudiated by vertebrate palæontologists, under the lead of Osborn, for the past half-century. Thus we find Mlle. Friant gladly accepting the "condylarth molar" as ancestral to the horse type just because the upper molar of *Phenacodus* includes six cusps arranged in three rows almost, but not quite, in accordance with her ideal archetype. But for the past thirty-six years (since Matthew's paper in the American Museum Bulletin, 1897) it has been on record that *Phenacodus* is the descendant of *Euprotogonia* (*Protogonodon*) and that the conical cusps and squarish molar contours of *Phenacodus* are less primitive than the more V-shaped cusps of the earlier condylarths, including *Protogonodon*. In *Ectocion*, a condylarth genus, as known from several species in the Wasatch Lower Eocene, the upper molars (Fig. 53) show a decided

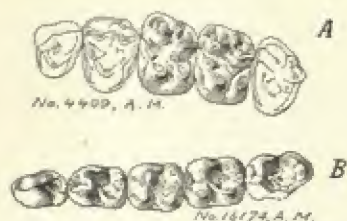


FIG. 53. A (upper) and B (lower) cheek teeth of a Lower Eocene condylarth, *Ectocion osbornianus*. Natural size. After Granger.

approach to the primitive equid (*Eohippus*) type in the relative prominence and oblique position of the crests on the protoconule and the metaconule. But not even this genus can be directly ancestral to the horse series, partly because it is too late in time, partly because the little crest on the metaconule does not extend forward and outward to meet the junction of the para- and metacones.

In selecting as her ideal archetype a rectangular molar pattern in which the anteroposterior slightly exceeded the transverse diameter, Mlle. Friant has assuredly gone counter to the evidence available in the case of the condylarths, artiodactyls and perissodactyls. For in the oldest known and, to the palæontologist, most primitive members of these

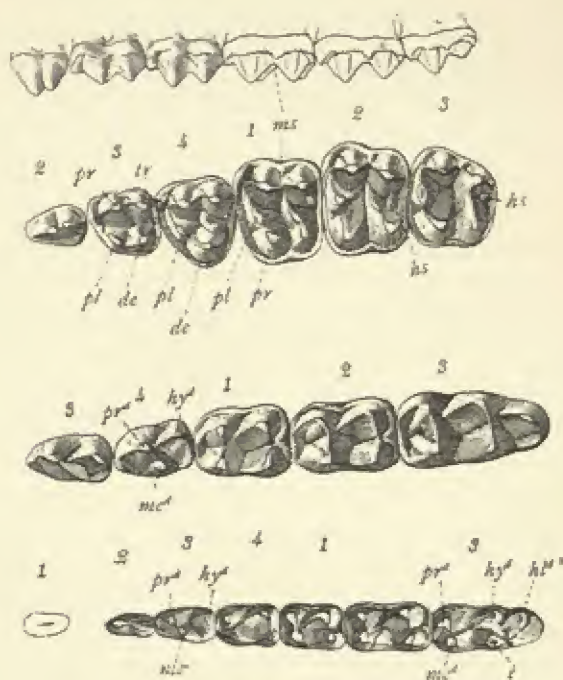


FIG. 54. Upper and lower cheek teeth of Lower Eocene ancestral horse, *Eohippus venticolus*. Natural size. After Wortman.

orders (Figs. 54, 55, 62) there are unmistakable traces of derivation from a tritubercular stage in which the inner or lingual border of the upper molar crown was shorter anteroposteriorly than the buccal border, and in which the transverse was greater than the anteroposterior diameter. Indeed the most primitive known member of all the condylarth families so carefully described by Matthew and Granger is the genus *Haplomylus* (Fig. 55) from the Lower Eocene

Wasatch of Wyoming, in which the tritubercular ground-plan of the upper molar is indisputable. And if Mlle. Friant had studied the primary documents of the case (published in the various Bulletins by Matthew and Granger), she would have learned that the Hyopsodontidæ, long classed as lemuroids and then as insectivores on account of the evident traces of the tritubercular ground-plan in their upper molars, were finally referred to the Condylarthra by Matthew and Granger because of the positive evidence afforded by the construction of the feet; she might also have seen that in *Meniscotherium*,

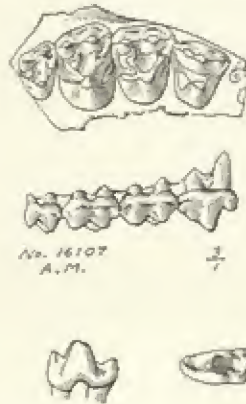


FIG. 55. Upper cheek teeth of primitive Lower Eocene condylarth, *Haplomylus speirianus*. $\times 3$. After Matthew.

representing another family of condylarths, the evidence of trigonalism, as we may call it, of the upper molars is unmistakable. If she had extended her observations further, she could hardly fail to have been impressed with the same phenomenon in the wide range of genera embraced in the family Periplychidæ of the suborder Taligrada, order Amblypoda (Fig. 56), which, although literally polybunous, are excessively different from the typical multituberculate ground-plan adopted by Mlle. Friant in the fact that the "protocone," to use the accepted name for this cusp, is not directly internal to the paracone but central in position so that the upper molar triad of main cusps has a trigonal symmetry.

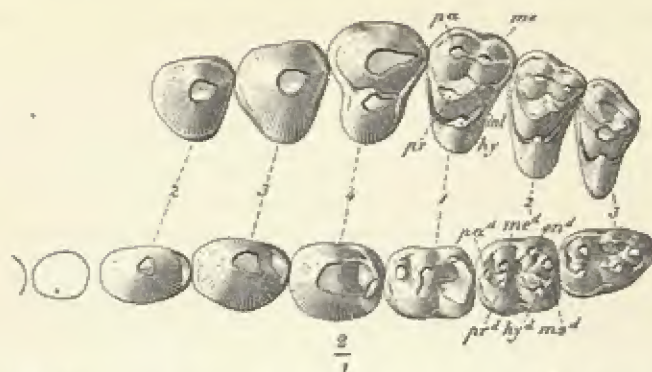


FIG. 56. Upper and lower teeth of *Conacodon entoconus*, a Basal Eocene (Puerco) relative of *Periptychus*. $\times 2/1$. Observe the reduction of the paraconid in the lower molars, correlated with the development of the hypocone from the basal cingulum of the upper molars. The upper molars remain tritubercular, although the protocone is somewhat pushed forward. The cusp marked ms^d is the hypoconulid. From Osborn, 1907.

Here we come directly to the crux of the whole question at issue between adherents of the polybunty theory of Forsyth Major and Mlle. Friant and the, by modern palæontologists, universally accepted theory of trituberculy, in so far as the latter doctrine proclaims the origin of the varied molar patterns of ungulates from an ultimately "tritubercular" or more properly trigonal ground-plan. For in Mlle. Friant's scheme (Fig. 57), since the ground-plan of each molar is

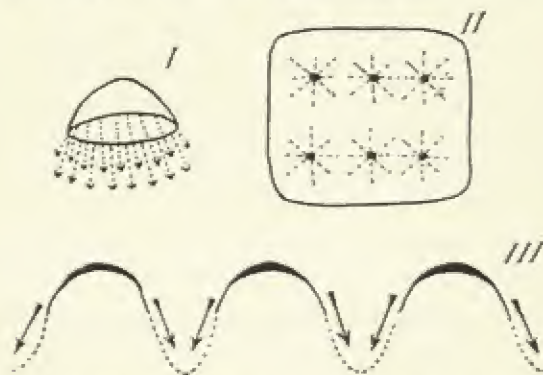


FIG. 57. Dr. M. Friant's hypothetical ground-plan of an upper molar. From Friant, 1933. I. A single cusp. II. The crown as a whole. III. Longitudinal section of forming cusps. The arrows show the direction of growth from the summit of the cusps outward and downward in all directions.

square, there are no notches or interdental embrasures on the lingual sides of the upper molars and the movements of the jaw in the ancestral stage are in any direction in the horizontal plane; but as a matter of fact and observation, in the more primitive ungulates of all known orders there are the most indisputable traces of a tritubercular upper and tuberculo-sectorial lower ground-plan, the significance of which becomes clear the moment we study actual specimens and put upper and lower molars into their proper occlusal relationships. In the relatively primitive Eocene titanotheres *Telmatherium cultridens* (Fig. 58), for example, we find that the protocone of an upper molar tooth fits squarely into the basin of the talonid of the corresponding lower molar, while the hypoconid of the lower molar fits between the lingual slopes of the para- and metacones, the protoconid of the lower fitting behind the lingual slope of the metacone of the preceding upper molar and in front of the lingual slope of the paracone of the corresponding upper molar,—all exactly as in the occlusion of the most typical insectivorous and carnivorous tritubercular-tuberculo-sectorial dentitions.

But Mlle. Friant is forced by her polybuny theory to make the unfortunate tactical blunder of denying that the hypocone is younger than the three primary cusps. This was easy for her to do since apparently she never considered either the direct evidence for the upgrowth of the hypocone in certain groups (*e.g.*, Hyopsodontidæ, Notharctidæ, Oxylænidæ, Arctocyoniidæ, Leptictidæ to Erinaceidæ, etc.) or the equally cogent evidence of the occlusal diagrams of the premolars and molars of various mammals as figured in my work on the Origin and Evolution of the Human Dentition (which apparently she has never seen). For when we study such occlusal diagrams of actual specimens we can hardly fail to note that there is indeed a progressive complication in the premolars of relatively primitive Eocene ungulates, such as *Telmatherium* (Fig. 58), whereby the typical tritubercular-tuberculo-sectorial relations retained in the premolars give place in the molars to modified tritubercular-tuberculo-sec-

torial relations through the upgrowth of the hypocone, which comes to fit into the valley of the primitive trigonid. And here we can also observe the lengthening of the anteroposterior diameter of the upper molars which supervenes in most ungulate lines and has the effect eventually of dividing the

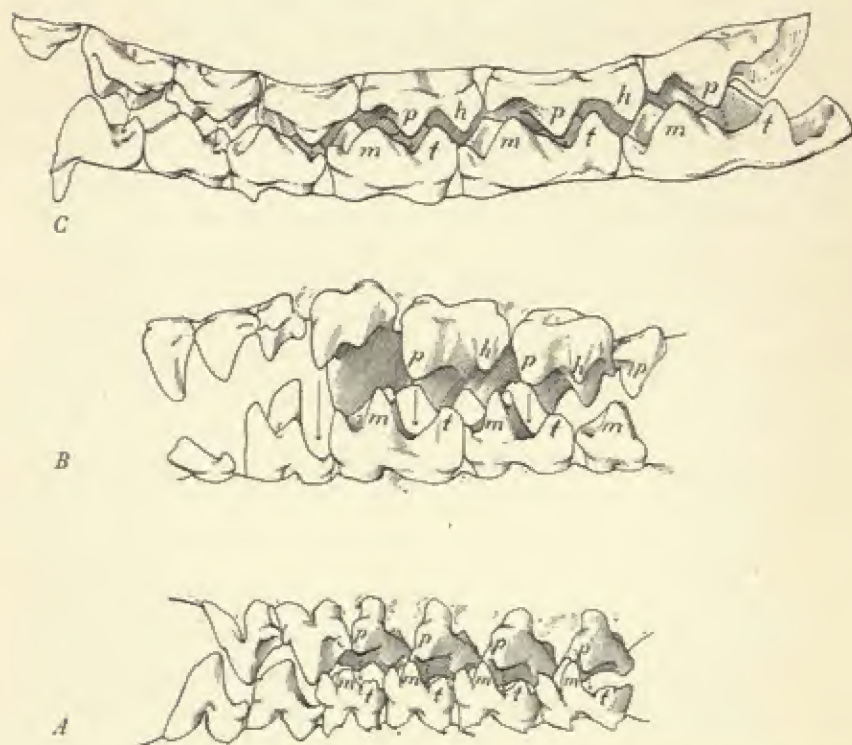


FIG. 58. Internal view of the cheek teeth (right side), showing that the protocone fits into the valley of the talonid of the corresponding lower molar, while the hypocone fits into the valley of the trigonid of the next succeeding lower molar. The para- and metaconid fit into the space between the upper teeth. A. *Didelphis*. B. *Erinaceus*. C. *Telmatherium cultrideus*, an Eocene titanotheres. *p* = protocone, *h* = hypocone, *m* = metaconid, *t* = talonid.

upper molar crown into two subequal anterior and posterior moieties which alternate with similar moieties in the shape of crests on the lower molars.

Pari passu with these changes in the occlusal patterns of the cheek teeth of primitive ungulates, we find a correlated

raising of the condyles of the mandible above the plane of the cheek teeth, a device which permits more lateral swing of the mandible and simultaneous engagement of the entire row of cheek teeth. This last condition has perhaps been acquired with the transformation of the premolar into the molar pattern in certain families of perissodactyls—a phenomenon recorded especially by Scott, Wortman and Granger, which may be verified in hundreds of fossil specimens in the American Museum of Natural History. Here we may observe the premolars passing from the essentially vertical or orthal relations of the tritubercular-tuberculo-sectorial ground-plan to various ectal, ental, palinal and propalinal excursions of the mandible in advanced ungulates and rodents, as these terms were long ago defined by Ryder.

There is another objection to Mlle. Friant's proposed solution of the problem of the ultimate origin of complex molar patterns of ungulates, which may be worth mentioning at this point. Her six-cusped, square-crowned upper molar is theoretically associated, as she states, with equal movements of the mandible in all directions in the horizontal plane. In such a mandible the incisors and canines ought also to be six-cusped or doubly triconodont exactly in accordance with the embryological "concentration theory" of Professor Bolk. But as a matter of fact the incisors and canines in all known "protoungulates" (condylarths, taligrades) and in all primitive perissodactyls (*Eohippus*, *Systemodon*, *Hyrachyus*, *Eotitanops*, etc. etc.) without exception are far nearer to the simple incisors and erect canines of Mesozoic and early Tertiary insectivores and creodonts, which have prevailingly orthodont vertical-oblique movements of the mandible and tritubercular-tuberculo-sectorial molars. It is only in certain excessively specialized notoungulates such as *Homalodontotherium* and some of the larger litopterns such as *Macrauchenia* that the incisors, canines and premolars are swept into a strongly polyisomeric series and even the incisors begin to take on premolariform patterns.

In some excessively specialized ungulates, including the horse, all three premolars of the cheek series have completed their transformation into the molar pattern (Fig. 59) and



FIG. 59. Upper cheek teeth of horses. After Matthew.

- 1 (top). *Orohippus*. Middle Eocene. Natural size.
2. *Ephippus*. Upper Eocene. Natural size.
3. *Parahippus*. Lower Miocene. $\frac{1}{2}$ natural size.
4. *Merychippus*. Middle Miocene. $\frac{1}{2}$ natural size.
5. *Equus*. Pleistocene. $\frac{1}{2}$ natural size.

even the deciduous molars, as is indeed the rule among mammals, are molariform. Here both interdental and intradental polyisomerism reach their climax as regards the members of the six upper cheek teeth on each side. The same is true also of the six lower cheek teeth, but in the horse, as in all other perissodactyls, the profound difference in fundamental pattern between an upper and a lower molar can be no other than a direct heritage from the contrast between upper and lower molars in the ancestral tritubercular-tuberculo-sectorial molars of still undiscovered proto-perissodactyls.

The opposite specialization, in which upper and lower molars tend to be alike, culminates in the elephants and mammoths, in which each upper and lower molar consists of numerous flattened plates closely appressed and submerged in a mass of "cement," which is deposited between and around the plates. In the later elephants the tooth succession instead of being "vertical" as it is in primitive tritubercular-sectorial animals becomes "horizontal," or more properly circular, since the newly formed teeth in the upper jaw move from behind downward and forward along the arc of a circle, finally being pushed out at the front as one after another of their vertical plates is ground down. And since this movement of replacement is always from behind, forward, the crowns are curved at the base in the rear of both the upper and lower molars. Consequently we never find the complete anteroposterior reversal between the patterns of opposite upper and lower molars which is characteristic of the many-plated molars of certain rodents.

In an excellent diagram (p. 106) Mlle. Friant traces the parallelism between the evolution of the plated molar teeth of Proboscidea and that of the many plated molars of rodents; then, completely deceived by the analogy, she imagines that she has established the close relationship of the two groups quite in the manner of Cuvierian naturalists of the 18th Century before De Blainville recognized the phenomenon of parallelism. But from a palæontological viewpoint the Proboscidea and Rodentia are widely separated orders of placental mammals with irreconcilable differences even in their dentitions. And while apparently admitting *Moeritherium* to be the most primitive of the proboscideans, Mlle. Friant does not seem to have noticed that its posterior premolars still conform to the essentials of the tritubercular-sectorial ground-plan in that the protocone of the last upper premolar fits into the talonid basin of the last lower premolar, or that its molars have reached a comparatively early stage of anteroposterior elongation and incipient doubling of the upper molar into like anterior and posterior moieties, or that,

in spite of this, one can still recognize the three primary cusps of the upper molars, which have their correct occlusal relations with the parts of the lower molars identified according to the nomenclature of trituberculy. Thus it may be said that at least in the premolars the most primitive proboscidean is the least polybunous and the least like Mlle. Friant's diagram of an ideal polybunous cheek tooth of six cusps equal in all directions.

The origin of the Proboscidea, one of the as yet great unsolved problems of vertebrate palæontology, is thus blithely settled by Mlle. Friant on the basis of a very partial resemblance in the pattern of the molars between rodents and proboscideans. In this connection it may be worth noting that some years ago, after making a systematic search of the literature for some known Lower Eocene type of mammal which might best have served as the starting-point for *Mærittherium*, the most primitive known proboscidean, I tentatively selected the small condylarth *Hyopsodus walcottianus* (Fig. 60) described by Matthew and Granger as having the largest observed number of favorable characters in the upper and lower incisors, premolars and molars as well as in the skull (supplied from *Hyopsodus paulus*). It so happens also that the pes of this form (described by Matthew and Granger) is relatively short and broad, and that the tarsals have the contacts which might be expected in the remote ancestors of the Proboscidea before the increasing body weight brought about the overgrowth of certain bones and their interlocking in the peculiar proboscidean pattern. No other known order seems to afford so favorable a starting-point.

In adding a number of accessory conules to their molar crowns the mastodonts parallel the wart-hogs (Fig. 61) among artiodactyls, *Desmostylus* among the Sirenia and *Eutypomys* among sciurormorph rodents. As these conules multiply and as the number of plates increases from the rear by the upgrowth of the posterior cingulum, the primitive intradental anisomerism of the tooth thus becomes sub-

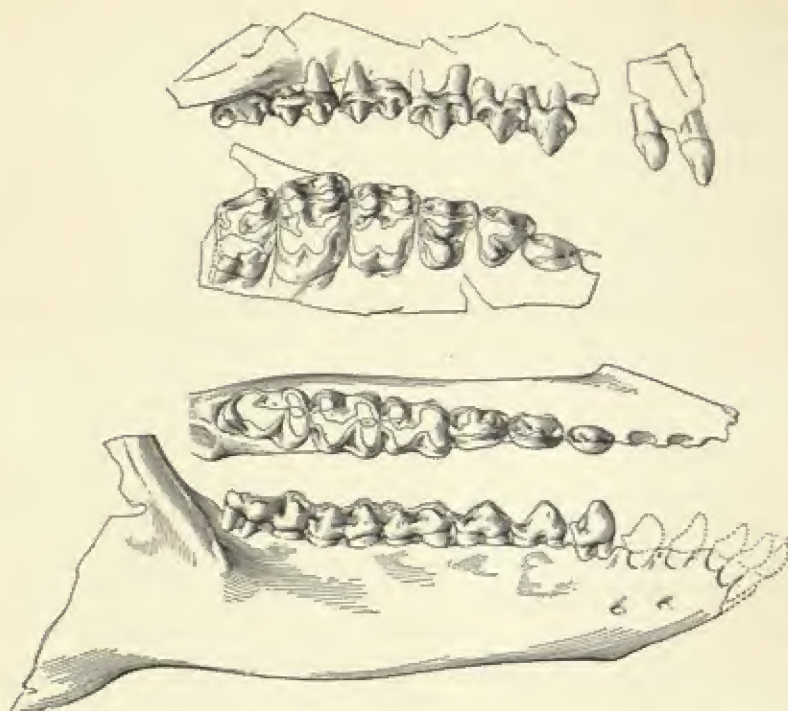


FIG. 60. Jaws and dentition of *Hyopsodus walcottianus*, Lower Eocene, Wyoming. $\times 3/2$. After Matthew.

merged in hyperpolyisomerism from two sources. Thus as time passes each proboscidean stage inherits the degree of polyisomerism attained by its parents plus the ability to generate still more conules, so that the effect is cumulative.

The artiodactyls conform beautifully to the standard for groups of tritubercular derivation, since one very early Eocene family, the Dichobunidæ, have almost pure tritubercular upper molars (Fig. 62), while even Stehlin, who is one of the most rigorous authorities in demanding fossils for evidence, admits a virtually tritubercular type as the starting-point for all the more advanced selenodont patterns in the entire order. Mlle. Friant, however, with a strong penchant for "polybunous" types, picks the modern hippopotamus as a central representative of the entire order. Now if the Hippopota-

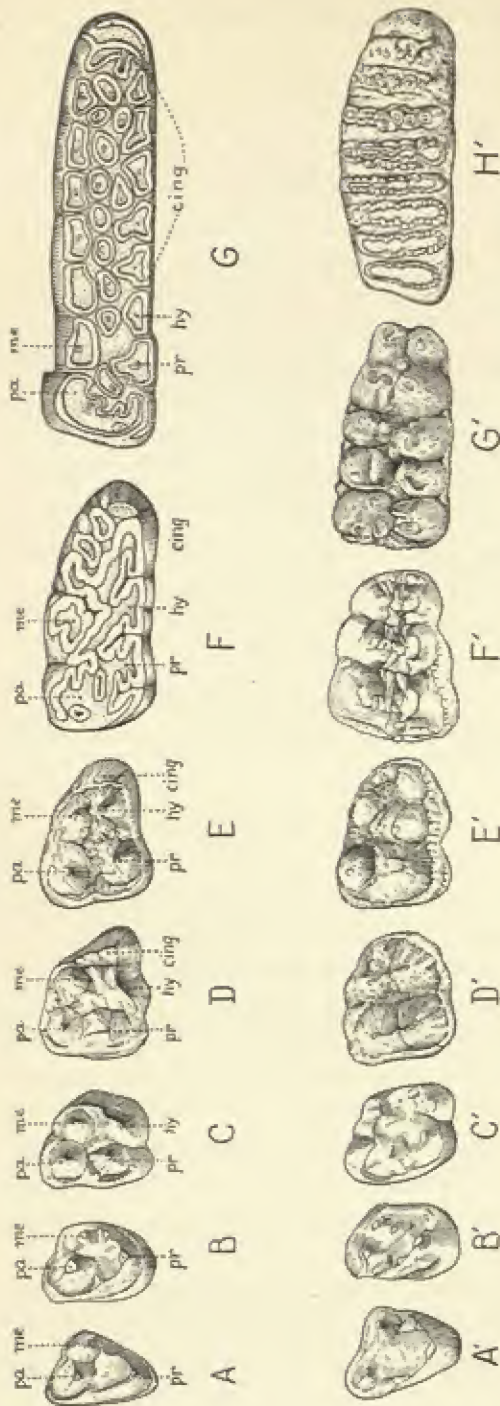


FIG. 61. Third left upper molars, indicating progressive secondary polyisomerism, with lengthening of anteroposterior diameter and addition of ridges and conules in the later forms. All reduced to same width.

- A. *Chriacus baldwini*. After Osborn.
 B. *Protogonodon pentacus*. After Osborn and Earle.
 C. *Palaeocherus typus*. After Stehlin.
 D. *Palaeocherus waterhousi*. After Stehlin.
 E. *Dicoryphocherus* sp. After Colbert.
 F. *Sus falconeri*. After Lydekker.
 G. *Phaenocherus* sp.
 A'. *Haplomylus speirianus*. After Matthew.
 B'. *Hyopodus penellianus*. After Matthew.
 C'. *Phenacodus primaeus*. After Matthew and Granger.
 D'. *Mastitherium gracile*. After C. W. Andrews.
 E'. *Palaeomastodon minor*. After C. W. Andrews.
 F'. *Serridinus anguivalis*. After Osborn.
 G'. *Mastodon xoulensis*. After Falconer.
 H'. *Stegodon bombifrons*. After Falconer.

After Gregory, 1934. Courtesy of National Academy of Sciences.

midæ are merely highly specialized offshoots of the suilline stem, then the double trefoils in their molars may be derived from such as are developed in certain fossil Suidæ, which in turn lead back toward the almost tritubercular teeth of the Cebochoeridæ. If, on the other hand, the Hippopotamidæ are the last survivors of certain Mid-Tertiary anthracotheres and related to *Ancodus*, as suggested by C. W. Andrews, then the hippopotamus molar has been derived from the most primitive anthracothere types, which are selenodont on their outer cusps and ultimately tritubercular in ground-plan. In either case the hippopotamus molar is almost as far as possible from the multituberculate atavus projected by Mlle. Friant.

Specialized Dentitions among the Carnivora, Pinnipedia, Cetacea.—Mlle. Friant, faithful to the principle of polybuny,



FIG. 62. Upper cheek teeth of primitive Lower Eocene artiodactyl, *Diacodexis chalcensis*, $\times 2$. After Sinclair.

selects the molar teeth of the bear as the central type for the order, never even mentioning the palæontological literature dealing with the question of the true status of the bears within the order. Schlosser and Matthew maintained that the bears are nothing but specialized dogs, while Gidley held that they represent an independent family derived from some early creodont like *Clænodon*. In either case, their elongate polybunous upper molar is a relatively late derivative from a form that unmistakably approaches the normal tritubercular pattern. The genera *Amphicyon*, *Hemicyon*, *Hyænarctus* and *Arctotherium*, although not altogether in a direct line, indicate very clearly that in the bears the carnassial tooth (p^1) has lost its pristine importance and greatly dwindled in size *pari passu* with the anteroposterior elongation of the molar (Fig. 63). But notwithstanding this marked specialization the anterior part of the trigonid of m_1 still shears against the reduced

FIG. 1 A

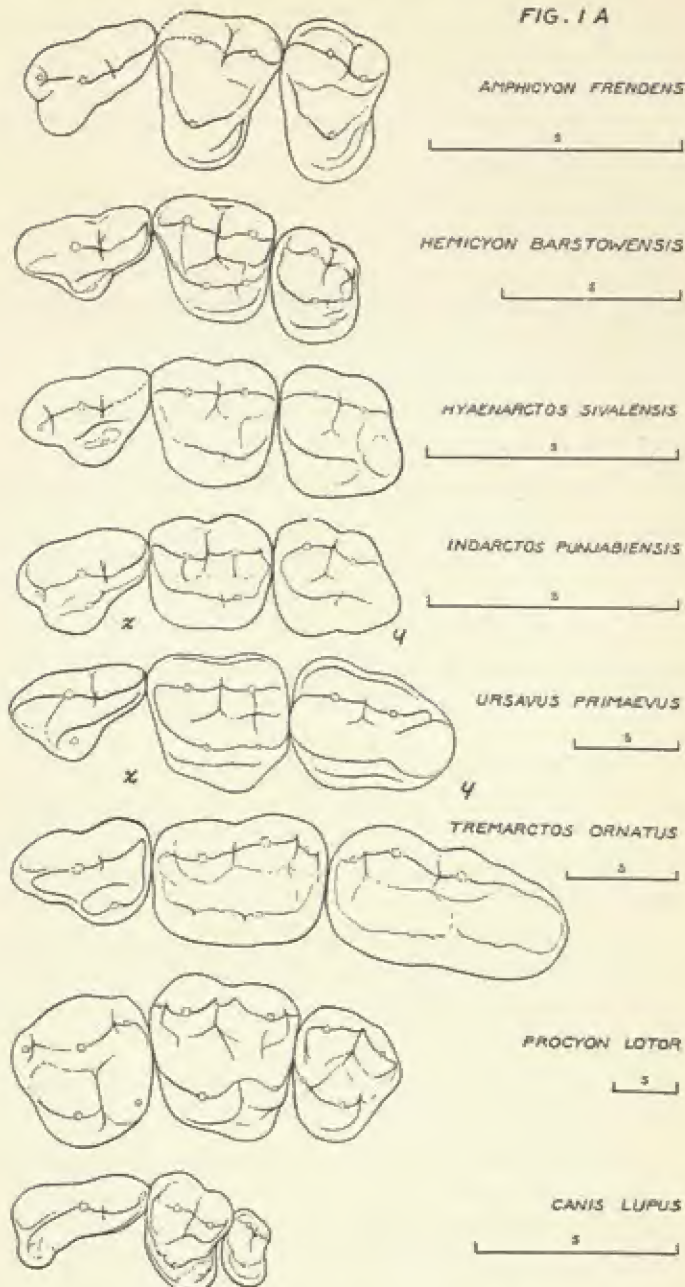


FIG. 63. Outlines of upper cheek teeth of giant dogs, bears and raccoon. After Childs Frick. Scales various: the anteroposterior diameter of p^4 (indicated by line s) in each case has been taken as the unit of comparison.

metastyle blade of p^4 precisely as in carnivores with normal carnassials. The polybunism of the remaining upper molar in the bears affords an example of extreme interdental anisomerism joined with intradental polyisomerism. By comparison with *Hyænarcus*, *Ursavus*, etc., it is seen that the greatly expanded inner shelf of the upper molar of the bear represents the merged protocone and posterior cingulum of the molars of the primitive dogs. Moreover a comparison of the locomotor skeleton of a bear with that of the more primitive dogs, raccoons and *Cynodictis* indicates clearly that the bear is a very highly specialized dog in which not even the famous plantigrade habit is really primitive as compared with the digitigrade habits of his relatives.

A loss of cutting power in the molars and the assumption of more or less polybunous form has occurred again and again among the Carnivora by steps which are reasonably clear to palæontologists. Among the Oxyclænidae the most primitive form, *Deltatherium* (Fig. 64), has a remarkably generalized



FIG. 64. Upper cheek teeth of *Deltatherium fundamini* Cope. From original specimen in the American Museum of Natural History. $\times 3/2$.

primitively polyisomerous dentition with small sharp cutting blades on all the molars, but from this central type we can trace a divergent evolution in one direction toward the extreme shearing blades of the Hyænodontidae and Oxyænidae and in the opposite direction (Fig. 65) toward the crushing molars of *Clænodon*, *Arctocyon* and *Anacodon*. Among the Mustelidae (Fig. 66) the earliest known types had already gone far in the production of an advanced shearing dentition (as in *Mustela*), but from this point onward many lines broadened the inner side of the remaining upper molar, culminating in the almost bear-like molars of *Taxidea* and finally in the great

polybunous crushing molars of the sea-otters. Even among the Viverridæ (Fig. 67), where the primitive dentition is of the cutting type, several genera acquire blunt cusps, like those of *Paradoxurus*.

The extreme shearing specialization occurs independently in several families of mammals; among the marsupials in the

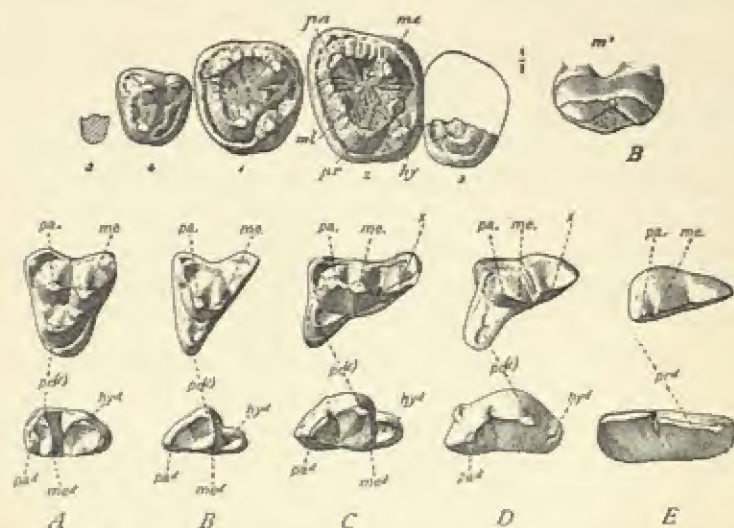


FIG. 65. Lower figure: Evolution of the sectorial upper and lower molars in creodonts, from a primitive tritubercular type. After Scott and Osborn. *Triisodon* (A) belongs in another series. B, *Sinopa*; C, *Oxyæna*; D, *Pterodon*; E, *Hyænodon*.

Upper figure: Cheek teeth of *Anacodon ursidens*. Natural size. After Osborn.

South American Borhyænidæ and in the Australian Dasyuridæ (Fig. 68); among placental Carnivora in the Hyænodontidæ and Oxyænidæ, Viverridæ and Felidæ. In all these cases great shearing blades are developed on the metacone-parastyle ridge of the upper molars and on the paraconid-protoconid shear of the lower molars; as these blades elongate anteroposteriorly they assume a more longitudinal position. Meanwhile the protocone of the upper molars and the talonid of the lower molars become reduced and in extreme cases disappear, thus completing the transformation of a primitive V-shaped upper tooth into a single notched blade.

A very curious specialization is found in *Proteles*, which seems to be a greatly degenerate termite-eating relative of *Hyæna* in which the teeth have dwindled to small points. Here we are again confronted by the riddle whether changes in structure precede changes in function or the reverse.

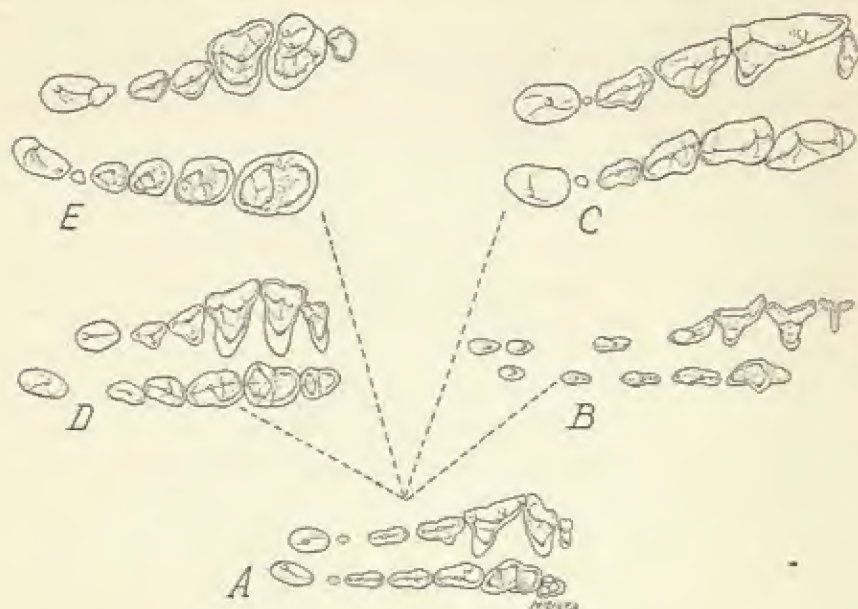


FIG. 67. Cheek teeth of Viverridae.

- A. *Genetta*, primitive type with shearing carnassial and sharp-cusped molars.
- B. *Eupleres*, with minute pointed teeth.
- C. *Cryptoprocta*, with shearing carnassial and reduced molar.
- D. *Suricata*, with widened molars.
- E. *Paguna*, with tuberculate carnassial and blunt-cusped molars.

In general we may say that in all the normal Carnivora there is a fair amount of interdental anisomerism with occasional instances of extreme intradental polyisomerism.

The opposite tendency toward secondary interdental polyisomerism is seen in the Pinnipedia, which for the most part have secondarily simplified cheek teeth varying from a pseudo-triconodont to a practically haplodont type. Among the toothed whales the more primitive *Eocetus* retains a slight

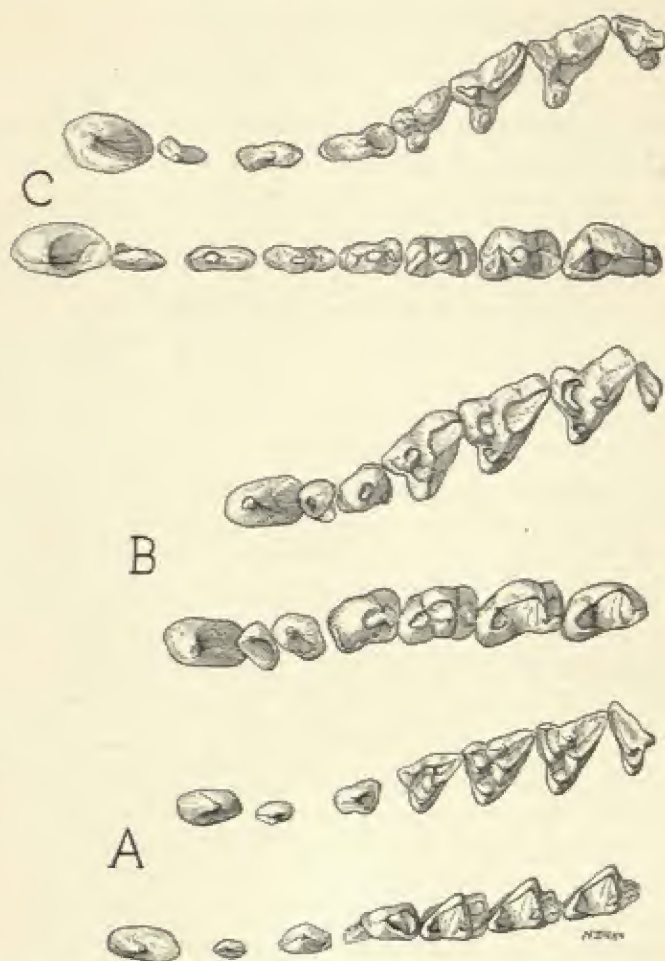


FIG. 68. Upper and lower cheek teeth of carnivorous marsupials. *A. Daryurus* $\times 3/2$. *B. Sarcophilus*. $\times 1$. *C. Thylacinus*. $\times 3/4$.

degree of interdental anisomerism from a *Hyænodon*-like creodont ancestor, but very rapidly polyisomerism becomes progressive in the extreme in the dolphins and finally retrogressive in *Kogia* or secondarily anisomerous in the narwhal.

Polyisomerism and Anisomerism in the Molars of Man

The present section is partly the result of one of the regular evening meetings of the staff of the School of Dental and Oral

Surgery, Columbia University (May 3, 1933), at which I was invited to discuss a paper read by Dr. M. Russell Stein, entitled "Some Variations of the Upper Third Molar."

In the course of his investigations Doctor Stein had started with the commonly accepted fact that in comparing the human incisors, cuspids, bicuspid and molars with each other, one can recognize various homologous parts and grooves in addition to the named principal cusps, and that these minor parts run throughout the series but with increasing emphasis as we pass from the incisors to the molars (Fig. 69). By examining large numbers of extracted first, second and third molars, he had then been able to show that between the extreme modifications of the third molars and the normal types there were many intermediate stages. He had also worked out a statistical interpretation of his findings. As each extreme form led back to the normal, there seemed to him no sound reason for regarding any one such extreme form, such as the so-called "triconodont" third upper molar, as a reversion to a primitive starting-point, rather than some other extreme, such as the "bicuspid" type of third upper molar. Doctor Stein was therefore inclined to protest against the tendency to call almost any such departure from the normal a "reversion," and expressed his scepticism concerning the adequacy of the theories of dental origin that were currently accepted in dental colleges.

In discussing Doctor Stein's paper I noted that the tendencies for canines to become like bicuspid and for bicuspid to become like molar and the reverse, were widespread among the dentitions of recent and fossil mammals of many orders. By means of lantern slides I showed several cases of convergence in pattern between premolars and molars and I stated that to the student of fossil and recent dentitions examples of de-differentiation were extremely numerous in every class of vertebrates and invertebrates. I congratulated Doctor Stein for his revolt against the doctrine of reversion as applied to human dentition and exhibited figures of a new set of enlarged models of recent and fossil stages in the evolution

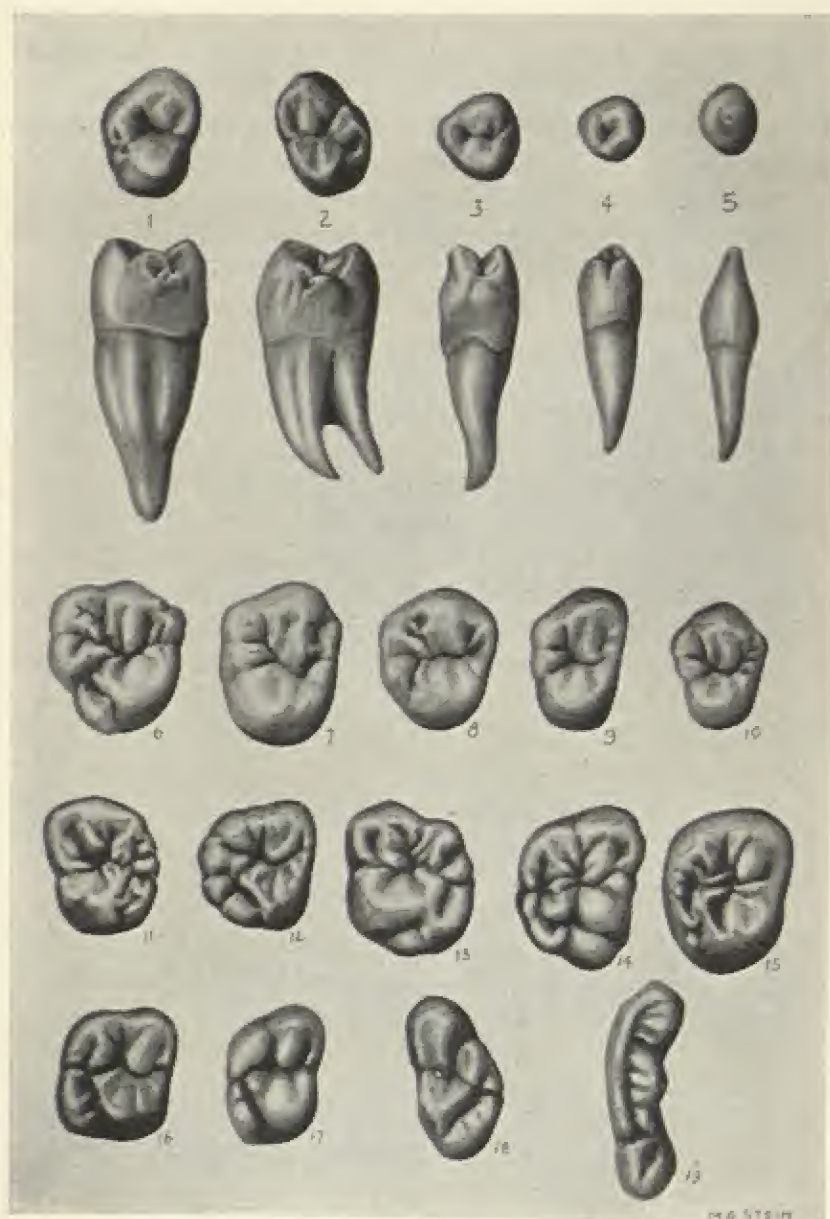


FIG. 69. Chart illustrating diverse types of third upper molars in man. After M. Russell Stein.

of mammalian teeth toward the human type, made at the American Museum of Natural History under my supervision, showing the constant interplay of tendencies toward de-differentiation of adjacent teeth coexisting with opposite tendencies toward differentiation.

In other publications I have discussed numerous examples of this phenomenon or mode of evolution, to which I have given the name of polyisomerism; the opposite process is called anisomerism. As an example: in the earliest and most primitive reptiles the teeth were numerous and all much alike—a condition of primary polyisomerism. In the line leading toward the mammals a period of regional anisomerism set in, culminating in the typical early Eocene mammals, in which the dentition was regionally differentiated into incisors, canines, premolars and molars. Then in the line leading to

First row: occlusal view of series revealing nature of the conical third molar.

Second row: distal view of same.

Third row: occlusal view of series showing the origin of the "bicuspid" type.

Fourth row: occlusal view of series of diverse types.

Fifth row: occlusal view of series showing the origin of the so-called "triconodont" third molar.

1. Upper right third molar, tricuspid pattern, trace of hypocone.
2. Upper left third molar, hypocone gone, trace of distal marginal ridge.
3. Upper right third molar, diminutive tricuspid pattern, no hypocone, no distal marginal ridge.
4. Upper right third molar, tricuspid pattern, loss of cusp differentiation, partial coalescence of cusps.
5. Upper right third molar, conical form, complete coalescence of cusps.
6. Upper right third molar, large distal marginal ridge, hypocone present.
7. Upper right third molar, no hypocone, marginal ridge same size as metacone.
8. Upper right third molar, protocone smaller than that of No. 7.
9. Upper right third molar, all parts smaller relative to paracone.
10. Upper right third molar, "bicuspid" type, diminutive metacone which is responsible for the bicuspid appearance.
11. Upper left third molar, disproportionally large paracone.
12. Upper right third molar, very large metacone and pronounced distal ridge.
13. Upper left third molar, disproportionally large protocone.
14. Upper right third molar, abnormally large tubercle of Carabelli, complete separation of the three lobules of the protocone.
15. Upper right third molar, vestige of distal ridge, diminutive hypocone.
16. Upper right third molar, well developed, looks like first molar.
17. Upper right third molar, same as No. 16 but shows some anteroposterior compression.
18. Upper left third molar, shows still more compression than No. 17.
19. Upper left third molar, greatly compressed, giving the appearance of a "triconodont" tooth.

the toothed dolphins there was an early tendency to obliterate the regional anisomerism and through degeneration to reduce all the teeth to single pointed crowns; meanwhile there was a rapid budding of the dental laminæ, producing a great increase in the number of the teeth and thus a condition of secondary polyisomerism.

I have recently discovered that this idea was partly anticipated by Cope in 1871, who applied the words "antero-posterior repetitive acceleration" to the multiplication of teeth, or to the anteroposterior budding of single teeth, while the process here called transverse anisomerism or transverse extension was named by him "lateral repetition" (*Vide supra*, p. 170).

Outline of Molar Stages from Fish to Man

Inasmuch as this paper is the tenth critical review of the origin and evolution of the tritubercular-tuberculo-sectorial dentition which I have published since 1907, when I assisted Professor Osborn in preparing the closing chapters of his book on "The Evolution of the Mammalian Molar Teeth to and from the Tritubercular Type," I may perhaps be pardoned for expressing a feeling of relief that the persistent obscurity of certain essential steps in the origin of the tritubercular molar seems at last to be cleared up, at least in my own mind, by the following interpretation of the facts.

This result, if accepted and confirmed by those qualified to do so, has been in no small measure due to the series of illuminating papers and memoirs by Dr. George Gaylord Simpson on the Mesozoic Mammals of North America, Europe and Mongolia; but since Doctor Simpson has consistently and courteously refrained from dealing with theories of the origin of the tritubercular molar except in so far as they were unavoidably and inextricably connected with his purely systematic and phylogenetic problems, it is due to him to state that while I hope and believe my conclusions are in accord with his unassailable facts and findings, yet he is not

to be held responsible for the following statements, which he may regard as falling short of certainty at the present time.

I am also under obligations to Mr. Frederick Thompson and Mr. Christopher Marguglio, who, under my direction in 1932, 1933, made a series of enlarged models representing ten stages in the evolution of the upper and lower cheek teeth, ranging from the pantotherian to modern man.

After this preamble we may say that, from present evidence, the tritubercular-tuberculo-sectorial molar type appears to have arisen in the following way:

First or Primitive Polyisomeric Stage.—At some very remote time, perhaps during the latter half of the Permian period, a small insectivorous mammal-like reptile possibly of the suborder Therocephalia, had polyisomeric and possibly polyphyodont simple recurved teeth on the margins of the jaws and perhaps clusters of small denticles on the roof of the mouth. The marginal teeth in the upper jaw overhung those of the lower jaw and alternated with them in spacing.

Second or Initial Cuspidate Stage.—Perhaps in Mid-Triassic times the descendants of Stage One developed one or more small accessory cusps on the slopes of the marginal teeth, transforming a simple recurved piercing crown into a jagged cuspidate crown (Fig. 35). This second or cuspidate stage is represented among the higher therocephalians in the genus *Cyrbasiodon* Broom.

Third or Protodont Stage.—In the third or protodont stage (Fig. 37) one of the higher mammal-like reptiles developed many submammalian characters in its skull and mandible, including reduction of the jaw elements behind the dentary. The dentition was clearly differentiated into incisors, canines, premolars and molars. The latter were compressed and sharp-pointed, with minute accessory cusps on the front and rear edges of the main cusp.

Fourth or Amphidontoid Stage.—In the fourth or amphidontoid stage (Fig. 40) the molar roots, hitherto single, have become divided into two, one behind the other. Both

upper and lower molar crowns form widely open triangles in basal section, with the apex internal in the upper, external in the lower. The main cusps (apices) are high and jagged, with accessory cusps or cuspules on their anterior and posterior slopes. The external cingulum is strong in the upper molars. The internal cingulum is more or less developed in the lower molars.

Fifth or Early Pantotherian Stage.—In this stage (Fig. 44) the main high protocone cusps forming the apex of the upper molar triangle extend toward the lingual side, changing the widely open triangle into an acute triangle with a V-shaped inner protocone tip. This changes the interdental embrasures from widely open inverted V's to narrow inverted V's. Meanwhile the lower molar trigons have shortened antero-posteriorly and widened transversely as they continue to fit into the narrowing upper interdental embrasures. Here we have a suggestion of the "rotation" of the paraconid and metaconid as originally conceived by Cope, but according to present evidence the upper triangle has not been formed by rotation but by inward growth of the protocone before the subdivision of the amphicone into the para- and metacones. In the lower molars a deep groove is formed behind the base of the trigonid and a small heel grows backward behind this groove, into which fits the tip of the protocone. The anterior premolars remain nearly simple, the last lower premolar, however, having an incipient heel and an internal cingulum rising below the site of the future metaconid.

From some early pantotherian or pre-pantotherian stage evolution diverged in two main directions, one toward the Cretaceous didelphid marsupials, the other toward the Cretaceous placental insectivores. In the first group the external cingulum and its cusps were greatly emphasized (somewhat as they were in the symmetrodonts), the metacone was often larger than the paracone and located well in toward the lingual side of the crown. The second line early gave rise to the

Sixth or Cretaceous Insectivore Stage.—Here the internally extended protocones have been reduced below the level of the

para- and metacones, which in *Deltatheridium* (Fig. 70) are seen to have sprung from a divided amphicone. The fourth upper premolar is incipiently molariform; in *Gypsonictops* the amphicone of p^4 is represented by two cusps (Simpson, 1929,

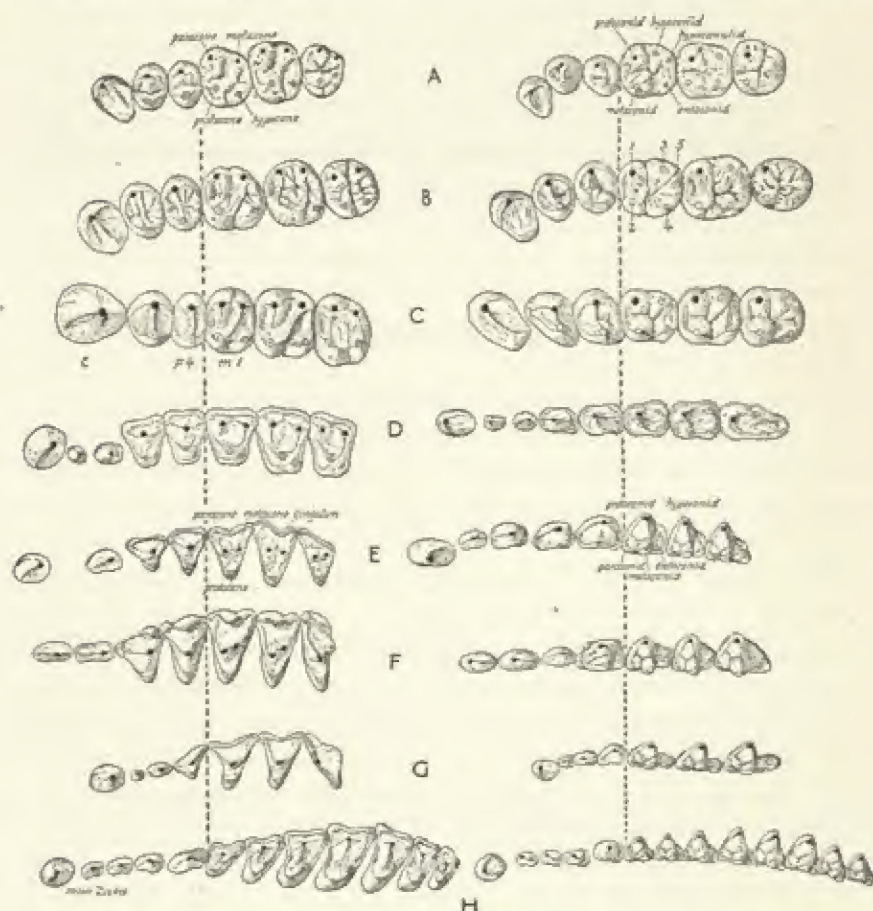


FIG. 70. Eight structural stages in the evolution of the cheek teeth in man. Scales various. A. Man (modern white). B. Le Moustier. C. *Dryopithecus*. D. *Pronycticebus*. E. *Didelphodus*. F. *Potamogale*. G. *Deltatheridium*. H. *Pantotherian*.

Fig. 21 (6)); in *Zalambdalestes* and *Deltatheridium*, however, it is still undivided. The anterior premolars are simple and it seems as if their tips represented either the amphicone or possibly both the amphicone and the protocone.

A side line leading to the modern zalambdodont insectivores started from near this point. It is represented by the Paleocene genus *Palaeoryctes* of Matthew, which has the upper molars (Fig. 21) extremely wide transversely and short anteroposteriorly with a great development of the outer part of the crown, so that the para- and metacones stand near the middle of the crown. The para- and metacones are barely separated. The lower molars have high trigonids and low transversely narrow talonids. In the modern *Potomogale* (Fig. 70F) the posterior premolars and molars are close to this stage, which adds to the evidence for the essential homology of the so-called deutercone or internal basal tubercle of the fourth premolar with the protocone of the molar.

Avoiding this specialized side branch, the main line gives rise to the

Seventh or Early Eocene Insectivorous Stage.—This stage (Fig. 70E) shows an incipient anteroposterior extension of the upper molars, which by this time have assumed the normal "tritubercular pattern" of many Paleocene and Lower Eocene placental families. This stage, however, retains many primitive features: the inverted V-shapes of the interdental embrasures, the strong development of the outer part of the tooth with distinct metastyle-metaconid shear, the relative narrowness of the talonid and complete tuberculo-sectorial character of the lower molars. Such a stage, probably already established in the early Paleocene, may have given rise to the

Eighth or Primitive Primate Stage of Pelycodus and Its Successors, Notharctus and Pronycticebus.—Here the upper molar cusps (Fig. 70D) become low and rounded, the protocones swelling and tending to reduce the interdental embrasures to narrow slits. As this takes place the hypocone buds off either from the posterior cingulum as a true hypocone or from the posterior slope of the protocone as a pseudo-hypocone. In the latter case the increasing entoconid grooves the protocone just in front of the incipient pseudo-hypocone. Meanwhile the growing talonid has widened transversely, becoming somewhat wider than the trigonid; its hypoconid fits between

the lingual slopes of the para- and metacones; its entoconid overlaps behind the protocone; its trigonid basin receives the tip of the hypocone or pseudo-hypocone. By this time the interdental embrasures have been nearly obliterated, the plan of the upper molar has changed from trigonal to nearly quadrate, the tuberculo-sectorial crown has lost its shearing trigonid, so that on the whole an oblique grinding action has evolved out of a nearly vertical shearing action. The premolars, while still four in number, tend to evolve into two groups, an anterior pair, progressively small, and a simple posterior pair, becoming bicuspid. This stage leads to the

Ninth or Anthropoid Ape Stage.—The upper molars (Fig. 70C), now with low conical cusps, tend at first to elongate anteroposteriorly; the paracones move to the outer side slightly beyond the level of the metacone; a strong crista obliqua connects the protocone with the inner ridge of the metacone. The hypocones become prominent. In the lower molars the expansion of the talonid, now bearing a hypoconulid as well as a low hypoconid and an entoconid, together with the loss of the paraconid, give rise to a five-cusped lower molar with the "*Dryopithecus* pattern" of cusps and grooves. The enamel surface of all the cones, especially in unworn specimens, becomes covered with minor enamel wrinkles and folds. The first two premolars having disappeared before this stage, the remaining two become bicuspid but the third lower premolar (now the second in number) is asymmetrical, more or less bicuspid, its oblique anterior face articulating with the enlarged upper canine. The canines, enlarged and tusk-like in the males, project much beyond the level of the other teeth. The incisors, with cutting edge, are more or less subdivided into cuspules.

A secondary shortening of the face and reduction of the canines gives rise to the

Tenth or Primitive Hominid Stage.—All molars (Fig. 70B) become rounded and shorter anteroposteriorly, the third beginning to diminish in size. The "*Dryopithecus* pattern" is often retained on m_1 , but is more or less replaced by the +

pattern in m_2 m_3 . The canines are small, not projecting beyond the level of other teeth but the chin is more or less sloping. The anterior lower premolar is bicuspid.

A further emphasis in the same direction gives rise to the *Eleventh, or Modern Human Stage*.—The third upper molars (Fig. 70A), with delayed eruption, are often reduced in size and in pattern, especially on the posterointernal corner. The lower molars decrease in anteroposterior length posteriorly. The plus pattern is normal on m_2 . The hypoconulid is often lost on m_2 , m_3 . The anterior premolars are losing asymmetry. The small lower canine is retracted beneath the overhanging upper canine, while the jaw has developed a chin. The lower incisal edge is often "tricuspid." Secondary polyisomerism is often evident in the development of similar small features on all the upper cheek teeth.

At each of the stages described above adjacent cheek teeth tend strongly to resemble each other in details although they may differ considerably in outer form. The resemblances in detail are an expression of the pervasive influence here called polyisomerism. This probably emanates from similar nutritional forces, from similar blood supply, similar nerve supply, similar endocrine influences and similar genic influences. It is as if at each stage all the molars became infected, so to speak, with a specific pattern which was, however, distorted by differences in growth rates of different parts, producing anisomerism, which again involves a complex of nutritional, mechanical, endocrinal and genic factors.

These principles are also exemplified in the dentition of man's nearest living relatives, the anthropoid apes. In the orang a strong tendency for the main grooves to break up into numerous fine-branching grooves pervades all the cheek teeth; in the gorilla there is an opposite tendency for the primary grooves to be emphasized, with an early wearing off of the secondary grooves; only the chimpanzee's teeth closely resemble primitive human teeth in the moderate character of the grooves and wrinkles as well as in the general pattern of the cusps; but all the apes retain the primitive length relations of m_1 m_2

m₃. The beautifully detailed and accurate studies of Remane on the dentitions of man and the anthropoids should, if sufficiently well known, settle for all time the relative nearness of the chimpanzee to man; while the studies by Pilgrim and by Gregory and Hellman on the dentition of the *Dryopithecus* group plainly indicate the phylogenetic source of these resemblances. The cries of "convergence" and "parallelism" which have been raised against this conclusion have never explained away the thousands of characters held in common by man with the anthropoid apes.

Present Status of the Theory of Trituberculy

In Dr. G. G. Simpson's two monographic revisions of the Mesozoic mammals of Europe and North America (1928, 1929) he was able to marshal strong evidence for the following results, here somewhat condensed and selected with reference to their bearing on the problems now under discussion.

(1) The genera *Menacodon* and *Spalacotherium* (Fig. 39), the lower molars of which had been selected by Cope as the basis for his theory of the origin of the tritubercular trigon by rotation of the para- and metaconids, were referred by Simpson to a newly recognized order which he named Symmetrodonta in allusion to the nearly symmetrical arrangement of the main cusps of the trigonid of the lower molars. These forms were contemporaries of the pantotherians, or Trituberculata of Osborn, in which the trigonids were asymmetrical. No evidence was observed either that the known Symmetrodonta had been derived from the Triconodonta or that they had given rise to the Pantotheria or Trituberculata, as was implied by the Cope-Osborn theory. Moreover, no evidence has been obtained for the migration of the para- and metacones around the protocones, either outward in the upper or inward in the lower jaw. On the contrary, there was some evidence, e.g., in the newly described form named *Amphidon* (Fig. 40) that the accessory cusp arose *in situ* on the slopes of the protocone or protoconid, respectively.

(2) Among the Pantotheria the name 'amphicone' was applied to a single undivided outer cusp (Fig. 45) corresponding to the undivided para- and metacones. It was also shown that in a much worn lower molar of *Amphitherium* a deep groove (Fig. 42) behind the base of the trigonid and in front of the small talonid ran sharply downward and outward. It was noted that this groove could have been made only by the movement of the lower jaw in sweeping across the protocone of the upper molar. It was pointed out (p. 243) that this fact had an important bearing on the general theory of the evolution of the molar teeth, but inasmuch as the author was purposely concentrating on the more immediate task of a taxonomic revision of the Mesozoic mammals, he refrained from further comment.

(3) By several series of comparative figures a basis was laid for the unexpressed inference that, in comparison with the upper molars of Cretaceous marsupials and insectivores, the amphicone corresponded with the para- and metacones and the main internal cusp with the protocone. Again, however, the important bearing of these comparisons upon the theory of evolution of the mammalian molars was not discussed, probably on account of the controversial nature of the subject as a whole.

Thirty-odd years of almost constant preoccupation with the problem, with prolonged and frequent reviews of the confusing evidence noted above, have led me to the following conclusions, which attempt to adjudicate between the rival parts of the premolar analogy theory and the original tritubercule theory but which leave still unsettled the claims of the embryology theory, as follows:

(1) The theory of reversed triangles arising by the rotation of the two accessory cusps outward in the upper, and inward in the lower jaw, lacks verification.

(2) The upper and lower molars, instead of being originally alike, have, at least since the earliest known stages, always been essentially unlike, especially in the sense that the uppers have always overhung the lowers and that the inner sides of

the uppers have always primarily engaged with the outer sides of the lowers.

(3) An *apparent* rotation of the accessory cusps in the Jurassic mammals has probably been brought about by the transverse extension of the upper crown carrying the tip to the inner side away from the external cingulum and from one of its offsprings, the amphicone. The same transverse extension of the lower molars, filling the narrowing inverted V's of the interdental embrasures, would induce an apparent migration or rotation of the paraconids and metaconids (Fig. 44).

(4) The protocone tips of the upper molars in the Jurassic *Amblotherium*, *Peralestes* and *Kurtodon*, are seen in Simpson's stereoscopic plates to be in anteroposterior line with the tips of the premolars; by transverse extension they were brought to the inner side of the molars. Similarly in the lower molars transverse extension shifted the tips more to the outer or lingual side as compared with the tips of the lower premolars (Fig. 44).

(5) Gidley's conclusion that in the Jurassic *Dryolestes* the internal upper molar cusp was a mere heel, arising *pari passu* with the talonid of the lower molars, may be the reverse of the true fact, which apparently was (Fig. 44) that the protocone tip of the upper molars grew inward, filling the interdental embrasures of the lower molars, encouraging the transverse extension of the trigonids and eventually calling forth the talonid of the lower molars, which arose as a stop behind the groove made by the protocone upon the base of the lower molar crown.

(6) In the Jurassic triconodonts, symmetrodonts and pantotherians there was a marked contrast, at least in the adult dentition, between the simple-tipped premolars and the more complex molars, both in the upper and lower series, exactly as noted by Osborn in his memoir of 1888.

(7) On the contrary, in the Upper Cretaceous insectivore *Zalambdalestes*, in the Paleocene insectivore *Palaeoryctes* (Fig. 21) and in all the later zalambdodonts there was such a

marked resemblance between the last upper molar and the first upper molar that one hesitates to ascribe this resemblance to convergence. In these forms as well as in all typical tritubercular mammals of the Paleocene and Lower Eocene the paracone of the molars has every appearance of being homologous with the tip of the premolars.

(8) Thus we have what may be called the premolar-molar paradox, that in the known Jurassic pantotherian mammals the protocone of the upper molars apparently accords with the Cope-Osborn identification as the homologue of the reptilian tip of the crown, whereas in the Upper Cretaceous and later insectivores and all later tritubercular placentals the functional "protocone" has every appearance of being a ledge cusp homologous with the deuterocône of the premolars. The final solution of the paradox, which may show that the known Jurassic upper molars belonged to wholly extinct families, may be revealed by future discoveries in the Lower Cretaceous.

(9) The subsequent molarization of the premolars, attained in various degrees by the Paleocene and later placentals, was in part convergence toward the molar pattern, according to the steps observed by Scott and all his successors.

(10) Since it was long ago shown conclusively by Wortman and later by Granger (1908) that even in two adjacent and very similar upper premolars (Fig. 15) of the same species of fossil horses (*Orohippus*) the posterointernal cusp may in p^3 represent the deuterocône and in p^4 the tetartocône, and since many other striking cases of pure convergence between p^4 and m^1 have been established in the ungulates, there still remains the possibility that at least in some phyla among Jurassic mammals, after the protocone tip had been displaced to the inner side, the contrast between the premolars and the molars became very sharp and so remained for long periods, and that when at last the necessity arose for molarizing the premolars the most convenient way proved to be not by displacing the premolar tip inward, as had been done in the molars, but by sending in from its base a spur or swelling

which gradually converged in shape toward the molar protocones; these had meanwhile been reduced in vertical height *pari passu* with the levelling of the trigonid with the talonid. In that case the resemblance between upper premolar four and molar one would be largely due to convergence.

(11) Meanwhile the posterior deciduous premolars, which in Tertiary and modern mammals are usually more molari-form than their permanent successors, in many lines also took up the path toward molarization, often at a faster pace than the true premolars.

SUMMARY AND CONCLUSIONS

Part I.—(1) After a half century of contention the Cope-Osborn theory of trituberculy seems to be justified in its main conclusion that in the upper molars of Mesozoic pantotherian mammals the main internal cusp represents the original tip of the crown. This result has been reached through a critical scrutiny of the evidence made available by G. G. Simpson in his most thorough taxonomic revisions of the Mesozoic mammals of Europe and North America.

(2) On the other hand, the theory of the origin of the trigon and trigonid by rotation of the para- and metacones toward the outer side of the upper, and toward the inner side of the lower molars is not supported by present evidence (p. 242).

(3) According to the transverse extension theory (pp. 212, 249) a modification of the Cope-Osborn theory of trituberculy proposed herein, the occlusal relations of upper and lower molars observed in later Mesozoic and early Tertiary placental mammals can all be accounted for on the following assumptions, in accordance with the evidence at present available:

(a) that in a still undiscovered pre-Jurassic stage the tips or protocones of the upper molars were progressively extended inward (Fig. 44), tending to fill the interdental embrasures between the lower trigonids;

(b) that the talonids arose as a stop to the inwardly-grown protocones (Fig. 44);

(c) that in a late Mesozoic partly known stage (Fig. 70G) the amphicone (derived from the external cingulum) divided into the para- and metacones *pari passu* with the transverse development of the talonid and the appearance of its outer cusp, the hypoconid;

(d) that the molarization of the premolars and of the deciduous molars in Paleocene and later epochs were later processes that finally in certain lines produced convergent but non-homologous identity of patterns between the upper premolars and molars.

(4) The "premolar-molar paradox," is that, whereas according to the evidence of the older Mesozoic mammals the original tip of the upper molars has been displaced to the inner or lingual side of the crown, the evidence summarized in both the premolar analogy theory and the embryology theory strongly appeals to the senses to accept the resemblances between corresponding parts of premolars and molars as indicating serial homology rather than convergence.

(5) The final resolution of this paradox may have to await the discovery of more Cretaceous mammals.

(6) Beyond the stage of the origin of the tritubercular molar the theory of trituberculy may be said to be supported by an enormous amount of direct palæontological evidence tending to establish the fact that even the most complex molar patterns of ungulates have been derived from the tritubercular type in strict accord with the steps postulated by Cope and Osborn.

Part II.—The main stages leading toward the human dentition from the lowest vertebrate type may be outlined as follows:

(a) In the "jawless" or agnathous stage, represented by the Silurian and Devonian ostracoderms, the minute food was probably sucked into the mouth cavity by the rhythmic depression of the floor of the mouth, the cartilaginous jaws

were barely if at all differentiated from the skeletal supports of the gill pouches, and teeth as such were not yet present.

(b) In the earliest gnathostome or true jaw-bearing stage, represented by Devonian elasmobranchs, the skeletal rods supporting the oral branchial arch began to function as jaws, while the placoid denticles of the skin around the jaws began to function as teeth. These at first were many in number and were unrolled from within over the edge of the jaws as needed.

(c) In the earliest bony fishes the cartilage jaws became encased in sheathing bones and the teeth on the dentaries and coronoids and on the premaxillæ, maxillæ, prevomers, palatines, etc., in the upper jaws acquired deeply infolded bases (labyrinthodont type) by which they were attached to the underlying bone.

(d) In the land-living vertebrates the teeth, at first not materially different from the preceding stage, gradually lost the labyrinthodont base and came to be attached in sockets to the premaxillæ, maxillæ and dentary bones, gradually disappearing from the other bones.

(e) In the mammal-like reptiles the teeth were differentiated into incisors, canines, premolars and molars, and were represented by two successional sets, corresponding respectively to the deciduous and permanent sets of mammals. The uppers overhung the lowers and alternated with them.

(f) In the line leading to the Jurassic pantotherians accessory cusps arose in the molars, the latter became markedly widened in the upper jaw, leaving inverted V-shaped interdental embrasures into which the lower molars fitted (Fig. 44). Thus by simple transverse extension the compressed jagged teeth of the higher mammal-like reptiles gave rise to the tritubercular-tuberculo-sectorial dentition of late Mesozoic mammals.

(g) The transverse extension of the upper molars undoubtedly carried the tip inward but in the Cretaceous and later mammals it is still unsettled whether the original tip is represented by the "protocone" of Osborn, on the inner side, or by the paracone of Osborn, which is more immediately

posterior to the tips of the premolars. At least in all the known phyla of Paleocene and Eocene placental mammals the paracone has every appearance of being the original tip, but at the same time the possibility that this is due to convergence should be admitted.

(h) From this point onward there is no substantial doubt as to the main stages leading to the molars of man (Fig. 70). In the upper molars the external cingulum became reduced, the para- and metacones moved apart as the anteroposterior diameter of the crown increased and as the hypoconid of the lower molar thrust itself in between the para- and metacones; also the hypocone grew up at the posterointernal corner of the tooth, gradually obliterating the interdental embrasure as the tooth lost its simple cutting character and took on the shearing-grinding function. Meanwhile in the lower molars the original trigonid, at first high above the level of the small heel or posterior spur, gradually sank to the level of the latter; it lost its paraconid as the hypocone of the upper molar developed. Then the talonid increased greatly in size, at first anteroposteriorly and then transversely, so that it finally exceeded the trigonid in transverse diameter. Meanwhile the cusps of the trigonid and talonid became low and rounded, while the fifth cusp or hypoconulid became very prominent, especially on m_1 . All these stages of evolution are well represented in known fossil primates. The *Dryopithecus* pattern of grooves and cusps on the lower molars first becomes conspicuous in the extinct anthropoid of that name but the pattern is often preserved in the first molars even of existing man.

The acquisition of the cruciate or plus pattern on the surface of the lower molars of man is associated with the loss of the fifth cusp and the secondary shortening.

The premolars, at first four on each side above and below, become reduced to $\frac{2}{2}$ in anthropoids; the bicuspid characters are gradually assumed in the chimpanzee, gorilla and *Dryopithecus*. The canines, which become tusk-like in male anthropoids, are much less prominent in female anthropoids and decidedly small in man. Rémane has amassed cumulative

evidence indicating that this is the result of a retrogressive process possibly associated with the delay in development and eruption of the adult canine in the ancestry of man.

In short, at this date 1933 there is little ground for doubting that the entire dentition of man has been derived from that of primitive anthropoids closely related to the Tertiary apes that ranged from Spain to India and from the Vienna Basin to South Africa.

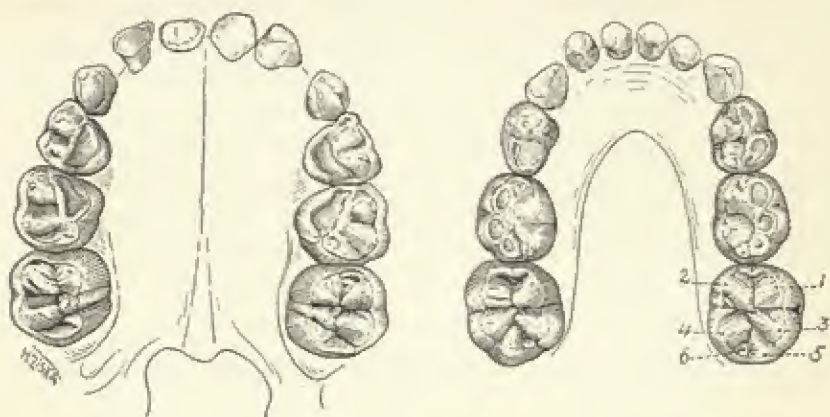


FIG. 71. Upper and lower teeth of *Australopithecus*. Natural size. Drawings based on casts and photographs, the latter kindly supplied by the describer of *Australopithecus*, Professor Raymond A. Dart. The hindermost teeth are permanent molars; the others are deciduous teeth.

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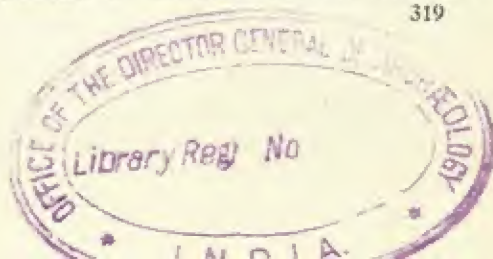
NEW FISHES FROM THE TRIASSIC OF PENNSYLVANIA

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(Read by title April 19, 1934)

ON the Norristown Quadrangle, Philadelphia Folio (No. 162 U. S. Geologic Atlas) an extensive belt of the Lockatong formation, Newark group, Upper Triassic, is indicated north of the city of Norristown. The town of North Wales is situated at the northerly margin of this belt, about seven miles northeast of Norristown. South of North Wales, about three quarters of a mile, the right of way of the Bethlehem branch of the Philadelphia and Reading railroad passes through a deep cut in the Lockatong, with an extensive spoil-bank of material excavated therefrom in its immediate vicinity, and from this debris dinosaur tracks and plant remains, including a species of *Podazamites*, have been collected by Mr. Edgar B. Howard of Philadelphia. A visit to the locality in March 1933 by Dr. Glenn L. Jepsen of the Department of Geology, Princeton University, in company with Mr. Howard, resulted in the discovery of a small Coelacanth fish, preserved in counterpart in fine-grained black shale. In the following October, additional material was secured by Dr. Jepsen, both of the Coelacanth and of an undoubted Elasmobranch. At present it is impossible to determine the precise horizon within the Lockatong from which these fishes came. All are in black shale and all were collected from the spoil-bank above mentioned. They were loaned to me for description by the Department of Geology of Princeton University through their discoverer, Dr. Jepsen.

The fossils in my hands consist of Coelacanth fishes and of sharks. Remains of Triassic sharks other than detached teeth and spines are extremely rare. I do not recall an instance in which they have been found in this country. Moreover, no indications of the presence of sharks have been found hitherto in the Triassic rocks of Eastern North America.



Accordingly, the discovery of an Elasmobranch fish in the Lockatong Triassic is of unusual interest, suggesting, perhaps, estuarine deposition.

Carinacanthus jepseni nov. gen. et sp.

Pls. I-IV.

Type: Skeletal remains from the trunk of an Elasmobranch fish in black shale (No. 13739 Prin. Univ. Pal. Mus.).

The type specimen (Pl. I) consists of the axial skeleton of the trunk together with two dorsal fin spines in natural position and the impressions of the pelvic fins. The head is unfortunately missing, no teeth are present, and only enough of the tail is preserved to show that it was of the heterocercal type.

In its present condition the fossil measures about 130 mm. in length and indicates a fairly small but comparatively long and slender fish. The cartilage of the visceral skeleton is strongly calcified in the peripheral layers and has a robust appearance. A low band of minute granular nodules appears above the neural spines, extending throughout the distance between the dorsal fin spines. These were possibly located in a fin membrane. A similar patch of granules appears in the lower caudal region. Here, they coalesce into vermicular lines forming a reticulate pattern. No other indications of shagreen are present, and no distinct actinotrichia are to be found.

The neural arches have been little disturbed (Pl. II). Each is composed of a stout, quadrangular basal portion from which arises a strongly developed neural spine. These spines are of nearly uniform height. As only the peripheral layers are calcified they appear as though hollow when crushed, with broad distal extremities. The basal portion of each neural spine is in contact with the base of the arch next succeeding, with no intercalaries intervening.

Below the neural arches lies a narrow, longitudinal vacuity, showing that the notochord was persistent and entirely unconstricted.

The haemal arches are shown only as impressions, except in the caudal region, where a few basal portions are preserved. Each of these is also in direct contact with its successor.

In the middle of the abdominal region, just below the axial skeleton, are ten or twelve short, slender, slightly curved impressions. These I interpret as having been made by the ribs.

Two complete dorsal fin spines are conspicuous in the fossil. The anterior dorsal spine is gently curved and measures 27 mm. in length. The basal portion of the spine is not distinctly demarcated, but measures about 7 mm. in length. At the distal end the spine is produced into a needlelike termination. This spine probably arose directly behind the pectoral arch. Its base appears to articulate with the tip of a neural spine, and is supported behind by a triangular cartilage also in contact with several neural spines. Seen in lateral view the anterior portion of the spine is strongly compressed, forming a cutwater. The posterior portion of the spine is thick and somewhat rounded, but there are no denticles on the posterior face. The outer layers of the spine are composed of trabecular dentine, causing the exposed lateral face to appear as though covered with fine, longitudinal striations. This appearance, however, may be due to abrasion. Other than this there is no trace of ornamentation on the spine. The extent of the pulp cavity is uncertain. Certainly it did not extend to the distal extremity of the spine, as shown by a fracture.

The posterior dorsal fin spine is placed near the beginning of the caudal region. It is about 45 mm. in length, curiously enough being far larger and more robust than the anterior spine (Pl. III). As in the anterior spine the base is not sharply separated, but measures no more than 10 mm. in length. The proximal end is opposed to a somewhat elongated neural spine. The supporting cartilage is not well preserved.

The exerted portion of the posterior dorsal spine is gently arched. It is broad proximally in lateral view and tapers to an acute point. The anterior portion is strongly compressed laterally, and forms a sharp keel or cutwater. The

posterior portion is thick and robust. There are no denticles on the posterior face. This spine also exhibits longitudinal striations on the lateral face, clearly caused by the trabecular dentine of which the surface, as now preserved, is composed. With its knifelike front margin and exceedingly acute termination one sees here a formidable little weapon of efficient design. Behind the spine are some patches of calcified fin membrane, but no definite actinotrichia are to be seen.

No traces of pectoral or anal fins are preserved, but in the pelvic region one sees distinct impressions of robust fin rays arranged in series and evidently caused by the paired pelvic fins, one of which is closely superimposed above the other (Pl. II). At first glance these fin rays might be mistaken for the elements of a single fin of the archipterygial type, but pelvic fins of this type are unknown in sharks. The upper fin in which the shape and natural arrangement of the endoskeletal radials are well shown has seven distinct rays of which the third is the longest. These rays are stout and rather broad. They are separated by intervals narrower than the width of the individual rays. The impressions of the basal elements of the fin are too indistinct for description. No fin membrane is preserved in connection with these structures which, no doubt, are of the ordinary Hybodont type. Five or six rays of the other pelvic fin can be seen, but they are not so well preserved. The origin of these fins lies opposite the space about midway between the first and second dorsal fin spines.

I believe there is ample justification for referring this shark to the *Cestraciontidae* although the unconstricted notochord and the comparatively large second dorsal fin spine are unusual features.

Another specimen in the collection exhibits a portion of the head of a small shark in which a jaw and teeth are the only recognizable features. This possibly may belong to the above described species (Pl. IV, No. 13824 Prin. Univ. Pal. Mus.). In this specimen there is to be seen the remains of a jaw bearing a row of obscure and imperfectly preserved teeth. These

seem to consist of a prominent central cusp flanked on each side by a single smaller cusp. The basal portions of these teeth are too imperfect for description.

Only an imperfect diagnosis of the genus *Carinacanthus* can be given at present. It is as follows: Fishes of rather small size and slender shape. Notochord unconstricted. Neural arches and spines robust and closely opposed. No intercalaries present. Ribs short and slender. Pelvic fins of the Hybodont type. Endoskeletal radials of these fins stout and not widely separated. Two dorsal fin spines present. Of these the posterior is by far the larger. Caudal fin heterocercal. Shagreen absent or consisting of fine granulations.

Coelacanthus newarki nov. sp.

Pls. V-VIII.

Type: A small fish preserved in counterpart in black shale (No. 13695 Prin. Univ. Pal. Mus.).

The type specimen of this little fish measures 71 mm. in length. It shows the body to have been rather deeply fusiform in shape. Only a few membrane bones of the head and opercular apparatus are preserved. The scales are missing as well as the pectoral and supplementary caudal fins.

At the anterior end of the fossil we find two large, broad bones each flanked behind by a rodlike element. This bends forward and downward expanding into a triangular plate. The anterior pair of bones is shown in visceral view and therefore belongs to the right side of the fish. The posterior pair is preserved in outer view and evidently belongs to the left side. I interpret the broad bones above mentioned as the opercula of the fish behind each of which lies the shoulder girdle of that side. Each girdle as preserved seems really to consist of two bones, the cleithrum and clavicle, attached to each other by overlap. The left operculum is ornamented with fine granulations. Below the operculum and clavicle of the right side lies a long bone, which I take to be a gular plate. The outer surface of this bone is exposed and bears an ornamentation of coarse, discontinuous, subparallel ridges.

Most of the head is missing in this specimen. However, another specimen in the collection (No. 13825 Prin. Univ. Pal. Mus.) exhibits a poorly preserved head seen from below. On this specimen the margin of a maxilla bears a single row of small, conical, widely spaced teeth, while the lower jaw is apparently toothless.

Returning now to our description of the type fossil, we find that as usual in Coelacanthids the notochord was persistent. The neural arches were widely forked, with high neural spines. These arches are only superficially ossified, leaving an internal cavity, the shape of which is shown on Pl. VIII, Fig. 2.

The haemal arches appear only in the caudal region and are not well shown in our specimens. They were similar in shape and size to the neural arches of that region.

In the front part of the abdominal region behind the shoulder girdle and above the pelvic fins are several large patches of thin bony tissue. These I suppose to be the remains of an ossified air bladder (Pl. VI). This bony tissue is too imperfectly preserved for detailed description. Another conspicuous feature of the abdominal region is found in the presence of a large number of pleural ribs. These are very long and well ossified.

No remains of the pectoral fins are found in the fossil. The pelvic girdles, however, are fairly well preserved and the impressions of a few lepidotrichia of a pelvic fin may be seen in the counterpart.

The plates of the pelvic girdles are situated opposite a point about midway between the anterior and posterior dorsal fins. Therefore, they must have been placed rather far behind the pectoral fins (PG, Pl. VI). The pelvic girdles are rather large, well ossified, and pentagonal in outline, with concave margins. No doubt, they were originally attached to each other in the ventro-median line. No traces of the segmented axis of the ventral fins remain and it is probable that these segments were cartilaginous or only slightly ossified.

The anterior dorsal fin is of relatively large size. Apparently it was situated directly behind the shoulder girdle

and well in advance of the pelvic pair. The endoskeleton of this fin consists of a large, ossified, triangular plate whose apex is directed downward and forward (BP₁, Pl. VI). The proximal ends of the lepidotrichia of this fin are forked to fit over the upper margin of the basal plate.

There are about ten stout lepidotrichia in the anterior dorsal fin. Of these the first seems to be the longest. All are perfectly smooth, expanded, but pointed distally and apparently unjointed throughout their length. It is quite evident that this fin was not lobed.

The posterior dorsal fin is located somewhat in advance of the anal fin. The basal plate of this fin is deeply forked, forming two processes of which the lower is the longest and lies between two neural spines (BP₂, Pl. VI). The upper anterior process seems to have been opposed to the lip of a third neural spine. The jointed axis of this fin is not preserved, probably having been cartilaginous. This axis must have had a length greater than the extreme length of the basal plate judging by the position of the lepidotrichia of this fin. The latter are shown only as impressions in the counterpart. They are smooth and delicate, but laterally expanded, with pointed tips. Only eight or nine of them are to be found and apparently they were unjointed. The arrangement is that of a lobed fin with radiate lepidotrichia.

The basal plate of the anal fin is placed about midway between the ventral lobe of the caudal fin and the pelvic girdles. It is similar in shape to that of the posterior dorsal fin being forked in the same way, but not so robust (BPA, Pl. VI). That portion of the plate posterior to the forks and against which the fin axis articulated is somewhat longer than in the second dorsal fin. A few slender rays of this fin are preserved in the counterpart. Judging by their position the segmented axis of this fin must have been quite long, but no traces of it remain.

It is extremely probable that the caudal fin consisted of three lobes. This is indicated by the vacuity formerly occupied by the notochord which extends mesially through the

tail and without perceptible contraction. The posterior "supplementary lobe," however, is missing in all of the specimens in which the tail is shown.

The endoskeleton radials of the caudal fin are expanded at each end to form articulating surfaces with the neural or haemal spines and with the lepidotrichia. They are robust but only superficially ossified (Pl. VII).

There are about twelve lepidotrichia in the dorsal lobe and approximately the same number in the ventral lobe. These lepidotrichia are laterally expanded, with smooth surfaces. They are jointed for only a short distance in their distal parts, four or five rather widely spaced joints being the greatest number found in any lepidotrichium. These joints are not well shown in the type fossil but may be clearly seen in another specimen shown on Pl. VIII, Fig. 1. Altogether, the caudal fin was a well expanded, powerful appendage.

Scales are not present in the type fossil, but in one or two other specimens a few detached scales are to be seen. Some of these are shown on Pl. VIII, Fig. 3. The ornamentation consists of four or five strong, widely spaced, longitudinal ridges.

This fish is easily distinguished from *Diplurus longicaudatus* Newberry, the only other Coelacanthid fish known from the Triassic of Eastern North America. *Diplurus* was a much larger, but proportionately more slender fish, with lepidotrichia unexpanded and jointed throughout the distal half, the anterior rays bearing acute spines. Also, the ornamentation of the scales differs considerably.

Coelacanthus, the type genus of the family, is still imperfectly known in many important features, especially in regard to the osteology of the cranium. It seems to me that the present fish, so far as can be ascertained from the condition of the fossils described herewith, presents no important features which would separate it from *Coelacanthus*. It certainly agrees well with that genus in many diagnostic characters, and there I would leave it until further information is available.

PLATE I



Carinacanthus jipuei nov. gen. et sp. Type specimen showing skeleton of trunk. (No. 13739.) $\times 14$.

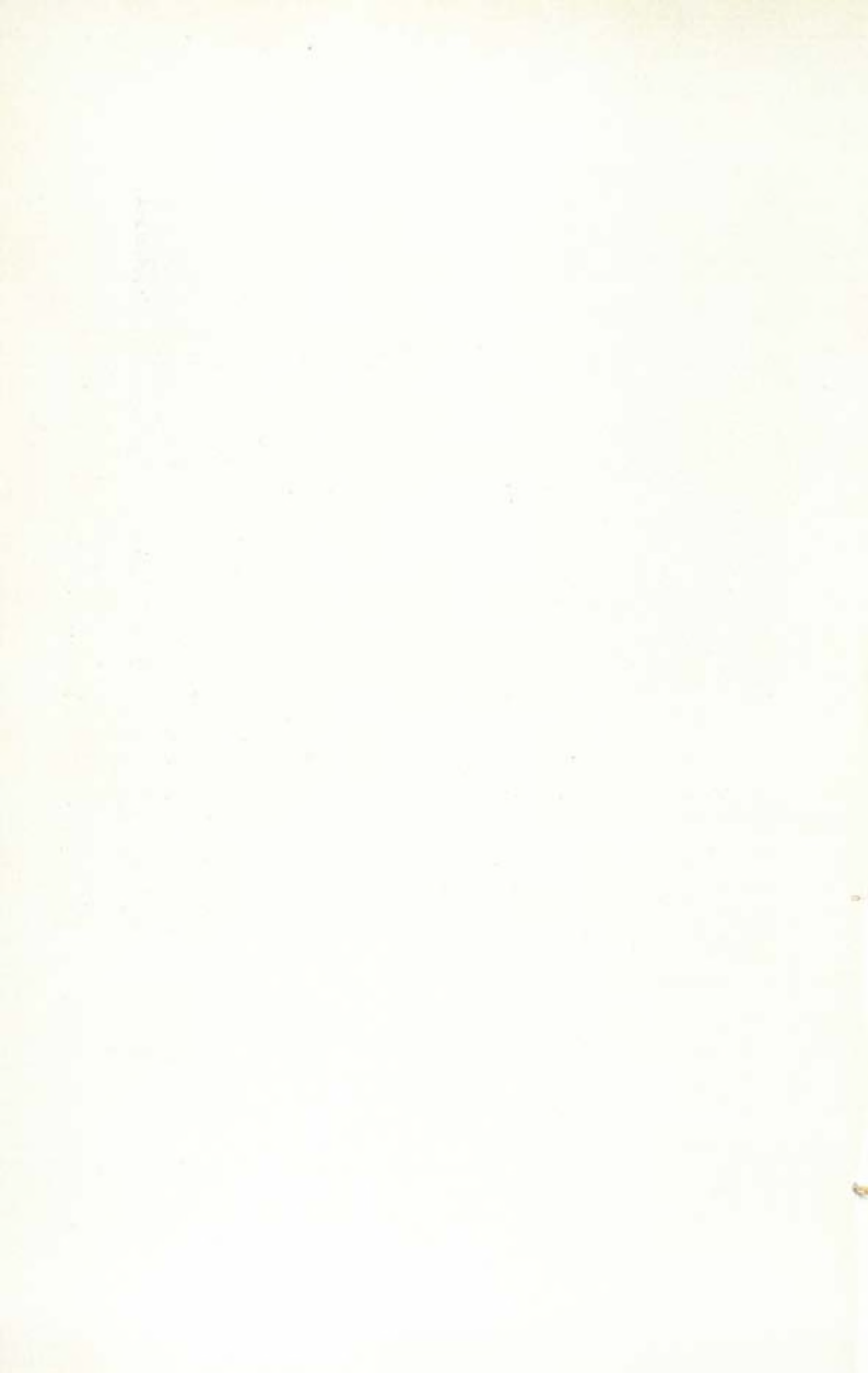


PLATE II



Carinacanthus jepseni nov. gen. et sp. Type. Neural arches, with impressions of pelvic fins.
(No. 13739.) $\times 4$.

PLATE III



Carinacanthus jepsoni nov. gen. et sp. Type. Second dorsal fin spine. (No. 13739.) $\times 3$.

PLATE IV



Carinacanthus jepseni? Fragmentary jaw showing row of poorly preserved teeth. (No. 13824.) $\times 53$.

PLATE V



Coalacanthus newarki nov. sp. Type specimen. (No. 11695.) $\times 2$.

BP₂

BP₁



BPA

PG

Cordacanthus nezarkii nov. sp. Type. Part of trunk showing pelvic girdles, anterior dorsal fin, basal plates of posterior dorsal and anal fins, ossified air bladder, neural arches, and pleural ribs. BP₁, BP₂, basal plate of anterior and posterior dorsal fins, respectively; BPA, basal plate of anal fin; PG, pelvic girdles. (No. 13695.) $\times 5$.

PLATE VII



Coelacanthus newarkii nov. sp. Caudal region of type specimen. (No. 13695.) $\times 4$

PLATE VIII



Fig. 1. Tail of fish. (No. 13826.) $\times 5$.



Fig. 2. Neural arches. (No. 13826.) $\times 4$.



Fig. 3. Detached scales. (No. 13825.) $\times 5$.

Coelacanthus newarki nov. sp.

NEW AMPLIFICATIONS OF THE NORTH AMERICAN PIPERACEÆ

WILLIAM TRELEASE

WHEN I discussed the geographic distribution of this highly complex and very puzzling family of plants before the Society, four years ago,¹ I segregated under the generic name *Arctotonia*² the North American species of Piperaceæ with pedicellate flowers which had been referred to *Ottonia* either as a section of *Piper* or as a segregated genus. As they were then known, the species ranged, on both sides of the continent, from Central Mexico to the old Continental break marked by Lake Managua between Nicaragua and Costa Rica. No indication has been found of the occurrence of an *Arctotonia* in the latter country, so that the genus appeared then to be as widely separated geographically from the true *Ottonias* as it is morphologically.

Though several as yet unpublished species of *Arctotonia* have been discovered since then, in the "Chicle" region at base of the Yucatecan peninsula, no recent collections modify the conclusions then reached as to the general range of the genus.

An extension of this range, however, is now unexpectedly offered by the unearthing in the Field Museum at Chicago of a specimen collected in Eastern Panama by Henri Pittier, in 1911, which appears not to have passed under the eye of Monsieur Casimir de Candolle when he worked over Pittier's other Panamanian and Costa Rican collections, and of which I saw no specimen when monographing the Piperaceæ of those countries subsequently.³ This plant, which is named here in honor of its discoverer, does extend the range of *Arctotonia* below the Isthmian continental break where the present

¹ *Proc. Amer. Philos. Soc.*, 69: 309, 1930.

² *L.c.*, p. 315.

³ *Contr. U. S. Nat. Herb.*, 26: 15, 1927, and 26: 115, 1929.

canal has been cut, though it offers no suggestion of a geographic overlapping of this genus and the South American genus *Ottonia*, the nearest known representatives of which are found in Venezuela and Trinidad.

ARCTOTTONIA PITTIERI n. sp.

A loosely branching glabrous shrub; flowering internodes short and slender, drying dark gray; leaves ovate, gradually long-acuminate, rounded at base or shallowly cordate and commonly oblique, $4 \times 8.5-6.5 \times 15$ cm., palmately 5- or characteristically 6-nerved, drying thin but somewhat rugulose; petiole 3-5 mm. long; flowering spikes 5×20 or 25 mm.; peduncle 5-8 mm. long; bracts subspatulate; pedicels somewhat longer than the flowers.

Type Locality: Alhajuela, Panama, at 30-100 m. (Pittier 3458, May 1911, at the Field Museum).

A decade ago, after examination of an important collection made by Ule, M. de Candolle¹ applied the name *Piper nudilimbum* to a shrub collected at Jurua Miry, Amazonas (Ule 5708) and elsewhere in the upper-Amazonian parts of Brazil. In general appearance, it is not unlike a number of species of *Piper* of the subgenus *Enckea*, for like them it has palmately nerved leaves; but it differs from them and resembles a small group of pinnately nerved *Artanthes* in having the stigmas borne on a short style as they are in the group called *Peltobryon* by Miquel many years earlier.

This synthetic species differs from all other known species of the *Pipereæ* except *Lindeniopiper*² in having its sympodial spikes, solitary or two at a node, borne on 1-bracted peduncles. This striking differential indicates the desirability of segregating it from the genus *Piper*, and the name *Pleiostachyopiper* is proposed for it with the following brief characterization:—

PLEIOSTACHYOPIPER n. gen.

Shrubs of the general characters of *Piper* §*Peltobryon*, but with the leaves palmately nerved and the subglobose spikes

¹ *Verhandl. Bot. Verein Prov. Brandenburg.*, 47: 113.

² *Proc. Amer. Philos. Soc.*, 68: 53, 1929.

1 or 2 opposite each subtending leaf, on a slender 1-bracted peduncle as in *Lindeniopiper*,—but with very different spikes and flowers (Plate *a*).

Type species, *Pleiostachyopiper nudilimbum* (C.DC.); *Piper nudilimbum* C.DC.

The third and concluding item in this short communication is even more surprisingly interesting than either of the preceding.

At the Botanical Museum of Stockholm there is preserved a collection made by N. J. Andersson something over eighty years ago, in part on or about the Isthmus of Panama which was then much frequented in the rush to and from the Californian gold fields.

One of Andersson's specimens, labeled as collected in Panama in April 1852, with multiple axillary spikes, is obviously of the *Pothomorpheæ*, or "*Piperæ* *Spuriæ*" as Miquel called them, and bears a close general resemblance to the typical genus *Pothomorphe* of that group: it differs markedly from all known representatives of that genus in its palmately nerved leaves—as in *Sarcorrhachis*¹ and *Manekia*²—which I have segregated in previous papers—though its inflorescence characters are more closely comparable with those of *Pothomorphe*. This segregable genus, named in honor of its discoverer, may be characterized as follows:

ANDERSSONIOPIPER n. gen.

Soft-wooded shrubs, with flabellately umbellate axillary spikes and palmately nerved leaves.

Type species, *Anderssoniopiper panamense*, with the following characters:

ANDERSSONIOPIPER PANAMENSE n. sp.

Apparently a moderate-sized half-shrub; glabrous; internodes 8 × 100 mm. below, shorter and slenderer upwards; leaves subreniform, typically abruptly short-acuminate, palmately 13- or 15-nerved with all of the nerves somewhat fine-

¹ Contr. U. S. Nat. Herb., 26: 118, 1929

² Fedde, Repert., Vol. XXIII, 313, 1927.

branched, $10 \times 9-15 \times 12$ cm., drying thin, paler beneath; petiole 3-6 cm. long, winged; spikes 2 (or more?) superposed in the axil, curved, in fruit 10×100 mm.; peduncle scant 2×10 mm.; bracts vague; achenes obpyramidal, the contracted apex protruding; stigmas 3, broad, sessile (Plate *b*).

Type Locality: "Panama" (N. J. Andersson, Apr. 1852, the type in the Botanical Museum of Stockholm).

Distribution: Isthmian region.

Like many other early collections, this species has not fallen under my eye in any other herbaria than the one noted, but there is little more surprising in the uncovering of a nondescript genus than of a nondescript species of a genus already known, in so diversified regions as the Isthmus and neighboring countries afford.

While this new genus is clearly distinguishable from all other known genera of Piperaceæ, its rediscovery must be awaited with more than usual interest, because there are reported contradictions in the labeling of Andersson's collections, so that while its characters are firmly established, the exact geographic source of the genus now named for him requires confirmation.

PLATE 4



Pleiotachyopiper nudilimbum, natural size. From a specimen collected at Soledad, Rio Itaya, Loreto, Peru, at an altitude of 110 m. (Killip & Smith 29562).

PLATE 6



Anderssoniopiper panamense, natural size. From the type, collected in Panama in 1852 (Andersson).

TURKISH REMAINS IN MODERN BELGRADE

J. DYNELEY PRINCE

FORMER AMERICAN MINISTER TO YUGOSLAVIA

(Read April 21, 1934)

"Belgrade enthroned on rivers twain hath watched the realms flit by."

IT is now known that for more than five thousand years, there have been continuous settlements at or near the confluence of the great rivers Danube and Sava, where the modern Belgrade stands. After the men of the stone age and the first Ægean culture, whose artifacts have been unearthed during the last three years by the excavations of Professor Ed. Vašić of Belgrade University, apparently there came Illyrians, a race of unknown provenance, succeeded by Celts, chiefly Goidhels, who gave to the city its former name Singidunum (Old Town, modern Erse: Sean-Dun). It will be observed that even in the Celtic days the place was "old."

Then came the Roman occupation for several centuries, mostly by the Flavian Legion. This was followed by two Gothic irruptions—Theodoric passed through once on his journey to Italy, and then there arrived the mixed Slavic horde known now as the "Serbs," who worked their way out of Galicia and have maintained themselves from the seventh century A.D. until today as the basic people, superimposed upon the other previous mixtures. Over the Serbs ruled the Byzantines at Constantinople—a régime broken by the short-lived Serb empire of Stefan Dušan and his congeners, to be followed by the Turks, interrupted again by the Magyars who eventually fled before the all conquering Moslem. For nearly four hundred years, except for brief Austrian occupations, the Serbs lay under the Turkish power, during which time Belgrade and its vicinity became an integral part of the Ottoman Empire, until the Serbs under Black George asserted

their partial independence in the first years of the nineteenth century and attained their full autonomy in the late 1860's.

This paper deals with the few Turkish remains which the hand of the Christian has permitted to survive. Even these relics are doomed to disappear rapidly under the modern hammers of the westernizing builders. It therefore seems worth while to record what is left of them in this "Year of Grace" 1933. I am indebted for most of the material to the excellent Bosnian Moslem scholar, Dr. Mehmed Remzi Deli , who is thoroughly familiar with the Turkish historical records and is himself the best authority on this subject in Yugoslavia.

In Belgrade proper, there are still four buildings in a state of more or less preservation, which date from the Turkish period viz., the only mosque which is still in use, the *Bajrakli*; the interesting tomb of Sheikh Mustafa—both these are in the city itself and outside the citadel; Damad Ali Pasha's tomb in the Upper Citadel; and the so-called "*Hammam* (Turkish Bath) of Suleiman" in the Lower Citadel. Some twenty kilometers south of Belgrade is the ruined Turkish fortress of *Avala*, which is a great attraction for visitors.

The description of these buildings follows:

THE *Bajrakli* (STANDARD) MOSQUE

The history of the one surviving mosque in Belgrade, the so-called *Bajrakli Djamija* (the Mosque of the Standard), is very confused. In all probability, during the period of the Austrian occupation of Belgrade from 1717 to 1739, the stone plate with the inscription over the gates was destroyed by fanatical hands, because it is evident that, during this period, the mosque was converted into a Christian church. This is clear, because the eastern and southeastern walls had been pierced for the purpose of erecting an altar and for making certain doors, no doubt leading to a now vanished vestry. Furthermore, the minaret which was of course demolished, was later rebuilt of a quite different material from that of the rest of the mosque.

According to the prevailing tradition, it is believed by many that this mosque was erected by Sultan Suleiman the

Lawgiver. Dr. Deliċ, however, thinks that there is a confusion of names in connection with this tradition, because the well-known Turkish traveller, Evlija Ćelebi, who paid a visit to Belgrade in 1660 and who has left us a detailed description of the city and its surrounding territory, mentions the names and founders of thirty-three important mosques, and he does not state that any one of them was built by order of Suleiman the Lawgiver, which he certainly would have done, had such a mosque existed in his day. In fact, he takes pains to state that there was a great Suleiman mosque in the upper citadel and yet another in the lower castle in the *Kala Megdan*. This citadel still exists, the chief part of it now being devoted to a Yugoslav military school. Evlija did not neglect many details in his description of the city.

The Austrians again occupied Belgrade in 1688 and on that occasion destroyed a large part of the place, including many of the mosques and other Moslem places of worship. After the sanguinary battle in October 1691, the victorious Turks restored Belgrade to something of its former state. All this took place during the reign of Sultan Suleiman II.

The mosques and *tekijas* were naturally among the first buildings to be reconstructed and it would be reasonable to suppose that, among the first of the mosques, would be one dedicated by name to the conquering liberator Sultan, vis., Suleiman II. The fact that the mosque we are discussing has for a long time borne the flag and the title "mosque of the standard" entitles it, Dr. Deliċ thinks, to the name "Mosque of Suleiman," not "the First," but "the Second."

This mosque was once encased in lead and its gate, which is at present covered with tiles, had originally two smaller cupolas encased in lead. The mosque remained for some time in a ruined condition, but it was repaired and restored during the reign of the liberally minded Serb prince Milan Obrenoviċ. Until the World War, the Municipality of the City of Belgrade to a great extent supported the Mosque, and its functionaries were appointed by the Serb Ministry of Educations and Cults.

At the present day, the structure is used for weekly Moslem services (every Friday morning) and last year it was the scene

of the official ceremony ordaining the Reis ul-Ulema, Maglajlić at which the Yugoslav King and most of the Chiefs of the Diplomatic Missions were present.

THE TOMB (*Türbe*) OF SHEIKH MUSTAFA

At the corner of Višnjićeva Street, just behind the Belgrade Municipal Building, stands the tomb (*türbe*) of Sheikh Mustafa, which was constructed in 1783. Here lies the body of the Sheikh, who belonged to the Order of the Sa'dis. This tomb was erected by Hüsni Effendi, the deputy of the then Turkish governor, and tradition states that the bodies of two other Sheikhs are also interred here, which is very probable, as it was the custom to bury several such notables together. I have personally inspected the three ancient Moslem coffins which occupy the middle of the round shrine.

This interesting building is still known in Belgrade as the *tekija* (Turk. *tekke*), as it was a part of an original religious house. Some writers assert that the first Serbian Minister of Public Instruction, Dositej Obradović, lived in the now vanished Moslem monastery, which enclosed this tomb and died there in 1811. Reliable records, however, do not connect either his life or death with the *türbe*. It is at least certain that he lies buried at the main door of the Orthodox Serb Cathedral. This association with Dositej is probably no more than an effort to throw some discredit on the most interesting Moslem relic in Belgrade. It is well known that there was, for a long time, a *tekke* (religious house) of the Sa'di order of Dervishes on the piece of land adjoining the tomb, which plot is occupied at present by other buildings and a portion of it is used as a dumping ground for material belonging to the Municipality. The popular name of the locality is still "*tekija*," after the original dervish house, no vestige of which except the *tekke* now remains.

While the *tekija* was in existence, the present *türbe* was in its spacious inner court (*avlija*). The old *tekija*-monastery was an extensive structure with a number of divisions and a large hall used for divine worship. All such buildings in the

larger towns were provided with numerous rooms for the accommodation of guests and pilgrims. It is, of course barely possible therefore, that a cultivated non-Moslem such as Dositej Obradović, might have lived, for a time at least, in such a house, but, as already remarked, there is no proof that he had any connection with the place.

Over the entrance to the tomb it is still possible to read the following inscription carved in relief and let into the wall on a stone slab over the door:

تطب عصر غوث وقت زیده اهل وفا
 موشد پر طریقت سعدی شیخ مصطفی
 جسع پاکندن ایدنه روح قوسی عزم حق
 ایلدی کلشنسرای هتئی دار الصفا
 تاعتمقام و دفتدی حسنی افندی دخی ایدوب
 تربه انساسله اولدی قطهر فیض خدا
 چققدی بر تاریخ جوهر نحسی حسن نام ایدوب
 مرقد گلزار قطب العصر شیخ مصطفی
 ۱۱۹۸

TRANSCRIPTION

Qutbi-asyr gavši vaqyt zübdei ehli vefa
 Muršidi piri tariqati Sa'di Şeih Muştafa
 Djismi pakinden idindje ruhi qudsi 'azmi Haqq
 Eyledi gulşensarayı djenneti dari şafa
 Qaimmeqam ü defteri, Hüsni Efendi dahı idüp
 Türbe insasile oldu mażhari feyzi Huda
 Çyqty bir tarihi djevher bahsi Hüsni nam edüp
 merqadi gülzari qutbulasyr Şeih Muştafa

TRANSLATION

Sheikh Mustafa, who was one of the disciples of the Chief (*pir*) of the Sa'di Sect, was the spiritual pole of the century; concentrated in his person was the salvation of his day; (he was) the *élite* of the faithful.

His sacred soul, leaving his pure body to go towards God, transformed the rose-palace of Paradise into a grove of joy.

Hüsni Efendi, the Prefect and General Finance Director, causing this tomb to be raised to him (Mustafa), has gained the favor of God.

A date according to the system "Djevher" was formulated giving (to the tomb) the name "Gift of Hüsni"

"Garden of roses of the pole of the century, Sheikh Mustafa"

= 1198

I am indebted to the Turkish Minister to Yugoslavia, Mr. Ali Haidar, for assistance in deciphering the above inscription and also especially in making out the system of indicating the date. There were two such systems of indicating dates in the old Turkish literature; viz., the simple method of adding up the total values of *all* the letters of the last line of a poem, and the present system *Djevher* (jewel), which showed the date by counting the numerical values only of such letters as had diacritical points. The total of these gave the date required. Thus, in the inscription cited above the letters of the last line were added as follows:

مرتد	-	ق	=	100
كلزار	-	ز	=	7
قطب	-	ق	=	100
قطب	-	ب	=	2
شخ	-	ش	=	300
شخ	-	خ	=	600
مصطفى	-	ق	=	80

Total: 1199

But, as shown by the words *tyqty bir* of the seventh line, the numeral "one" (*bir*) must be subtracted, which gives the correct date; 1198 A.H.

I have not employed the modern system of writing as used by the Ghazi's Government, as it is quite inadequate to indicate the original consonantal values.

DAMAD ALI PASHA'S TOMB (*türbe*) IN THE UPPER CITADEL

It was formerly generally believed that the bones of the celebrated Kara Mustafa Pasha lie in the tomb (*türbe*) which is still to be seen in the upper citadel of Belgrade. Mustafa Pasha was the great Vizir and Generalissimo of the Turkish forces who was executed in Belgrade after the defeat of the Turkish arms before Vienna. Others believed, however, that this tomb contains the remains of Hadji Mustafa Pasha Šinikdji, known by the jocular epithet of the "Serbian Mother," whom the well known Belgrade *dahiye* (refugees) killed in this fortress. It is highly likely that this latter version has made it possible for the tomb to remain practically intact till the present day, as this pasha was a great benefactor.

These theories are, however, quite without foundation, for according to the Turkish sources, it is regarded as an established fact by Dr. Delić and other scholars, that this tomb contains the body of Damad Ali Pasha, the conqueror of the Morea, the son-in-law of the then Sultan, and the Grand Vizir and Generalissimo of the Turkish army, who was killed in the battle against Eugene of Savoy on August 13th, 1716, at Petrovaradin. His remains were brought from there and interred in the court-yard of the great Mosque of Suleiman I, then in the upper citadel. This tomb was erected for him alone (but see below). This mosque of Suleiman I was very large and encased in lead. The celebrated Turkish architect Mimar Sinan was proud of it and praised its slender, tall, artistically constructed minaret.

After the Austrian attacks of the seventeenth century, had destroyed this "glorious building," the Turks erected in its

place in the upper citadel the so-called "renovated habitation of Sultan Mahmud I."

It is interesting to note that in 1846, the body of the Belgrade vizir, Tepedelenli Selim Pasha, was interred in the same *türbe* beside the body of the great Ali Pasha. To those with a sympathy for old Turkish culture therefore, this tomb is of especial interest because in it lie the remains of the great, generous anti-corruptionist generalissimo Ali Pasha and his deservedly famous successor, Tepedelenli, who was noted for his justice.

Until the time of the World War, over the entrance to this tomb there stood an inscribed plate which was greatly mutilated. The inscription consisted of two lines and a half-line underneath them which indicated the date. The only words we know of the inscription were those at the end of the first line, viz. "Ali Pasha," and "Mustafa Pasha" at the end of the second line. The Turkish scholars conclude that the words "the late Ali Pasha" stood here and that it was stated that Mustafa Pasha "built the tomb."

Towards the end of the World War, a bomb fell upon the tomb and partially destroyed it. The soldiers of the Austrian occupation, however, carefully repaired it as well as possible, and left it in its present condition.

Dr. DeliĆ remarks as follows regarding Mustafa Pasha who, as noted above, is supposed by some to be buried in this tomb: Inasmuch as Kara Mustafa Pasha was executed as a criminal, it is not to be supposed that he would be buried at the gate of the Suleiman mosque and, furthermore, that a "türbe" would have been erected to him. In the City Museum at Vienna there is a skull, said to be that of Kara Mustafa. This is probably not genuine. One record states that the severed head of Mustafa Pasha was preserved in salt and taken to Jedreni where the Sultan then was, and that the head was interred in the cemetery of a mosque, under the windows of the former palace of Kara Mustafa. Here a stone stood, and probably still stands, bearing the inscription—"The head of Merzifunli Mustafa Pasha who was unjustly decapitated."

It is likely that this is the genuine resting place of the head of the unfortunate great commander.

THE TURKISH BATH (*Hammam*) IN THE LOWER CITADEL.

An ancient Turkish bath is still to be seen in the Lower Citadel of Belgrade. The records show that in the year 1660, there were two such *hammams* in Belgrade, the larger one having been that of Sultan Suleiman. The bath which is in existence to-day, although it is undoubtedly of Turkish construction, is not identifiable as having been the Suleiman *hammam*.

HAVAŁA (AVALA)

Avala is the castle of the well known Turkish military leader Porča which is on the summit of the hill Žrnovo (commonly known now as Avala mountain, some twenty kilometers south of Belgrade. Near the top the Serbs have erected the tomb of their Unknown Soldier. The word *havalā* is Arabic adopted by the Turks in the sense "dominating point." According to Turkish sources, the fortress of *Havalā* was built by the Turks during the reign of Sultan Murad II (1421-1451). Certain notes state that Murad built this fortress in collaboration with his father-in-law, the despot George Branković Smederevac, in order that Belgrade should be kept under observation from this point. The city, according to the treaty after the death of the despot, Stefan Lazarević, had passed into the hands of the Magyars. When the Magyars under Hunyadi Janos (Sibinjanin Janko) later penetrated into the heart of the Balkans, this fortress was abandoned. In 1456, Ghazi Porča Mahmud Pasha Abogović took possession of it and established a garrison in it which was kept up with the object of watching the military operations around Belgrade.

This garrison undertook frequent attacks on the Magyars and, according to the Turkish chroniclers, returned from these forays "to their nest with prisoners as numerous as a flight of falcons." Even after the occupation of Belgrade again by the Turks, a small garrison was maintained for a long time

in this little citadel. Evlija Čelebi, writing in 1660, states that this fortress has a commander with a force of fifty men and several cannon with a suitable quantity of munitions which were stored deep down in the earth. There were also here one mosque, five houses, several cisterns for water and a very narrow courtyard. The remains of the cisterns and the courtyard are still traceable.

The grave of Porča, the first commander of the fortress known to us by name, lies not far from the castle, a little above the new hotel on Avala. Before the world war, this grave was enclosed by a stone structure, of which at present there remains only a single stone. The Austro-Hungarians, removed this fence, as they dug their trenches alongside the grave and probably even through the grave itself. The building of the new hotel caused the unearthing of numerous skulls, evidently many of them older than the world war. My Moslem chauffeur not long ago picked up one of these remarking sadly: "Perhaps this was the great Porča."

The place where this grave was is now one of the sights of the Belgrade region.

Finally, it should be mentioned that the building now occupied by the Belgrade Art Museum, which was founded by Prince Paul of Yugoslavia, is said to have been originally a Turkish Municipal building. Unfortunately I can find no records regarding this picturesque structure but it is quite possible that the tradition regarding it is correct.

In honor of my Teacher and Colleague, Professor Richard J. H. Gottlieb of Columbia University, New York City

THE DISTRIBUTION AND ORIGIN OF THE WEST INDIAN AVIFAUNA

JAMES BOND

(Read Dec. 1, 1933)

A GROUP of islands lying between two great continents and separating two of the world's zoological regions must perforce be of interest to naturalists and thus the West Indies have received more than their share of attention in this field. But as far as I am aware no intensive and intimate survey of this area has been undertaken in any one branch of natural history by any one person. Partly on account of this and partly because of the great changes that have taken place and are taking place in the fauna of these interesting islands, I began in 1926 an ornithological survey of this entire region, visiting over fifty islands and studying in the field over 170 of the 180 odd genera of West Indian birds. The results of this survey were of interest in many ways; perhaps the most important was in being able to throw some light on the affinities of a number of the endemic genera and species. The bird life of the islands can now be considered very well known and there are in all probability no further indigenous species awaiting discovery.

The actual limits of the West Indies may be somewhat difficult to define geographically, but from the point of view of the ornithologist, the limits of this region are comparatively well marked, being comprised of the Greater Antilles, including the Cayman and Swan Islands, the Lesser Antilles and the Bahama Islands. Trinidad and Tobago are definitely South American and other islands of the Caribbean Sea, such as the islands off the north coast of Venezuela, including the Dutch Islands of Curacao and Aruba, and the island of Cozumel, off the coast of Yucatan, have certain West Indian affinities, but had perhaps best not be included

among the West Indies. One is rather tempted to include the small islands of Old Providence and St. Andrews, which contain several races of West Indian species and no genera not found in this region.¹ It must be admitted that the constitution of the West Indies, as just defined, is based entirely on bird life and I am aware that herpetologists, entomologists, botanists and others may reach different conclusions, but the remarkably distinct ornithological fauna of this region indicates possibly better than any other branch of natural history the true limits of this faunal area, since out of some 122 resident genera of "land birds" in the West Indies, more than fifty are endemic to this region or are at least of Antillean origin.

Now as I have mentioned the West Indies lie between two zoogeographical regions, the Neotropical, which has by far the richest avifauna of any part of the world, and the Nearctic region which for its size has the poorest. One might thus believe that the West Indian islands would have derived most of their bird life from the Neotropics, to be predominantly Neotropical, and indeed they are considered by zoölogists to comprise a sub-region of the Neotropical region, rather than of the Nearctic. But from a study of the bird life, this appears to be an erroneous conclusion. Of the 62 families of birds recorded from the West Indies, only two, the Potoos (*Nyctibiidae*) and the Cotingas (*Cotingidae*), are not found in the United States. The Potoos are represented in the Greater Antilles by one species, which is found in Hispaniola, Gonave Island and Jamaica, but is not specifically distinct from a species ranging widely through Central and South America. The single Cotinga known from this region is restricted to Jamaica

¹ It has been noted that several birds of the Dutch islands in the south Caribbean show an affinity to Virgin Island forms but I believe this to be the result of similar environment rather than an indication that these islands were formerly connected.

The occurrence of West Indian birds on these extralimital islands of the Caribbean was in all probability brought about by their being blown there during some severe storm or hurricane. The fact that some are not found on the mainland is no criterion for saying that they have never reached the mainland. Rather it is more than likely that they have reached Central or South America but through competition of allied forms were unable to establish themselves.

and, though a distinct species, is a member of a wide-ranging Neotropical genus, which significantly is the most northern ranging genus of the family, having even reached as far north as Arizona, although it is not yet known to breed in the United States. Of 178 resident West Indian genera, including all birds breeding in the West Indies, 45 are of world-wide distribution or at least range widely beyond the confines of the Americas, 52 are found in both North and South America, 19 are Neotropical and 8 Nearctic while as many as 54 are endemic to the West Indies.

Fundamentally as far as I have been able to judge, the West Indies are Nearctic in their bird life. The Antillean species of North American genera are in many cases relicts, while the purely Neotropical forms are closely related to continental species, indicating a more recent arrival. These latter are naturally most numerous on the islands nearest to South America, *i.e.*, Grenada and St. Vincent. It appears to me that the important relict fauna of the West Indies is probably much like that which formerly existed in northern Central America and owes its preservation to isolation by means of water barriers. Central America, since the land bridge of the Isthmus of Panama was formed, has received an influx of Neotropical forms which has no doubt had an effect on the original fauna. On the other hand a number of Central American birds reached South America in this way, among which were the Motmots, the nearest relatives of the West Indian Todies, which originated somewhere in northern Central America.

The almost entire absence of Neotropical families of birds in the West Indies is really remarkable when it is considered that these are well represented on such islands as Trinidad and Tobago. Indeed, adding these two islands to the West Indies would nearly double the number of indigenous genera of birds of all the Antilles and Bahama Islands combined, and add as many as 14 Neotropical families to the region. I might mention that the Parrots (Psittacidae), Trogons (Trogonidae) and Thicknees (Burhinidae), all represented in the West Indies,

are not Neotropical families, all occurring for instance on the continent of Africa. The subfamily of Piculets with two New World genera, one of which is restricted to the West Indies, is also represented by a genus in West Africa and another in the Far East; and the Greater Antillean Palm Swifts have their nearest relatives in Africa and the Far East.

If we examine the peculiar genera of West Indian birds, we find that many are closely related to North American forms, and it seems likely that a number of our North American genera are of West Indian origin or vice-versa. For instance the genus of Wood Warblers, *Dendroica*, the largest and most diversified genus of bird in North America, is not represented by one endemic Central or South American species, yet the genus is very well represented in the West Indies, not only by species closely related to those of North America, but by some very peculiar species of uncertain affinities, at least one of which (*Catharopeza* of the Island of St. Vincent) has been considered sufficiently aberrant to be classified as a distinct genus. There are two endemic genera of Tyrant Flycatchers in the West Indies, *Tolmarchus* and *Blacicus*; the former is very close to the Kingbirds (*Tyrannus*) but is not closely related to the South American *Pitangus*, as is frequently suggested, while the latter in my opinion should be considered congeneric with our Wood Pewees. The peculiar West Indian family of Palm Chats, *Dulidæ*, is of uncertain affinity but is believed to be akin to the Waxwings, a Holarctic family, comprising but three species, two of which occur in North America. The two endemic West Indian genera of Swallows are closely related to the Tree and Violet-green Swallows of North America. The three endemic genera of Thrushes are related to North American Thrushes. The Thrashers and Warblers, characteristic Nearctic families, are each represented in the Antilles by no less than four peculiar genera. The Hispaniolan and Jamaican Vireos, *Laletes* and *Lawrencia*, are both I find merely representatives each of a group of West Indian Vireos and are related to the White-eyed Vireo, and others of this genus in North America. One

of the most interesting birds found in the West Indies is the White-winged Crossbill, a boreal species of the Hudsonian Zone of North America and also found in northern Europe. The discovery in 1915 of this finch in the high pine forests of Hispaniola was remarkable, but illustrates still further the relationship of West Indian birds. Another interesting finch, discovered at the same time in the mountains of the Dominican Republic, is the Andean Song Sparrow, a species found in the mountains of southern Mexico, south along the Andean chain to the Argentine, with another insular race on the Dutch Islands of the south Caribbean. This species, until recently considered as a monotypic genus, is now regarded as a member of the North American genus *Zonotrichia*, rightly, I think, although it is also and perhaps more closely related to the North American Song Sparrows, *Melospiza*; but it seems to be certainly of northern origin.

It will be seen therefore that a large number of the peculiar West Indian genera are related to North American birds, but there are a number that have evidently been derived from Central America, this element being perhaps strongest in Jamaica.

The relationships of the various islands of the West Indies are worth considering. In the first place the region is easily sub-divided into three provinces, the Greater Antilles, the Lesser Antilles and the Bahama Islands. Of the three, the Greater Antilles are the richest in bird life, though the Lesser Antilles have as has been mentioned many endemic forms.

The smaller islands of the Greater Antilles have no peculiar fauna; thus the birds of the Isle of Pines are those of Cuba, the birds of Gonave Island, those of Hispaniola and so on. The Cayman Islands are, however, more interesting. The largest island, Grand Cayman, has received most of its bird life from Jamaica and Cuba, whereas Little Cayman and Cayman Brac have derived theirs from Cuba alone, indicating in this case that the smaller islands are of more recent origin. On the other hand, the fact that a number of birds are found on Grand Cayman which do not occur on the smaller islands

is no sure criterion that they never occurred there, since there are many species which would be unable to find a favorable habitat on Little Cayman and Cayman Brac. This condition is particularly apparent in the Grenadines and on the Bahama Cays. For instance a number of species are found on St. Vincent and Grenada but are lacking in the Grenadines due to unsuitable environment. Thus it is a good rule when exploring a group of islands to choose the larger ones for intensive work, since the smaller ones are apt to be disappointing.

The Lesser Antilles show a fairly uniform bird fauna with the remarkable exception of Martinique. To the north and to the south of Martinique are found a number of species lacking on this island, where, however, they are represented by distinct species of these same genera, some at least of these distinct species having their nearest relatives in Central America. I can account for this only by believing that the present island of Martinique is older geologically than the remainder of the Lesser Antilles, and that the peculiar species of the island represent older types, the existence of which prevents an incursion of allied species. I should like to explain this by taking as examples two Flycatchers of the genus *Elania* which occur in the southern Lesser Antilles. One of these birds *E. martinica* is a distinctly West Indian species, with a remarkably disconnected range, occurring throughout the Lesser Antilles, west to the Virgin Islands and again reappearing on the Cayman Islands, islands off the coast of Central America, Old Providence and St. Andrews Islands, and the Dutch Islands in the south Caribbean. The other bird, *E. flavogaster*, is a continental species ranging from southern Mexico to the Argentine. Both these birds are very closely related, so it is of interest to see what has taken place where their ranges overlap. The continental species is evidently a recent arrival on Grenada and St. Vincent, since it has not yet become subspecifically distinct from the dominant South American race, but it has become established on Grenada long enough to have had a pronounced effect on the status of the West Indian bird, the latter being now entirely confined

to the high mountain country, while the continental bird alone is found in the lower, more arid districts. On St. Vincent the continental bird has evidently not been so long established, since the two species are found side by side in the lower country, where, however, the continental bird is rapidly becoming the dominant species, forcing the West Indian form into the mountains, as in Grenada. Whether eventually the West Indian bird will entirely disappear from these islands is problematical, but it may hold its own in the mountain forests. I mention this as a possible explanation of altitudinal distribution in representative species which is so well known among Andean birds where one species will range to perhaps 6,000 feet elevation where another representative species will take its place. This has been attributed to ecological and temperature factors, but I am convinced that it is caused in many cases by the presence of closely allied species that prevents any overlapping of ranges. Usually where the ranges do not overlap the birds are considered geographical races or subspecies, but this is, as I have explained, not always the correct explanation and can be solved in many cases only in the field. For instances the two Lesser Antillean *Elænias*, although almost identical in structure and color pattern, have very distinct habits and notes. I have little doubt that this competition between allied forms is the cause of the Antillean *Elænia* and other West Indian birds having failed to become established in Central America, although they can persist on many of the small islands off the coast.

The West Indian Nighthawk, though representative of the common Nighthawk of the eastern United States and very similar in coloration, is in reality a very different bird, and should probably be considered specifically distinct, although even the most conservative of our systematists regard these birds as subspecies. On the other hand representative forms differing widely in color pattern have often similar habits and songs and would probably interbreed if their ranges met, examples being the Cuban Warblers of the genus *Teretistris*, and the Hispaniolan Tanagers of the genus *Phanicoophilus*.

Such interbreeding is known to take place with two Warblers of the eastern United States, the Blue-winged and Golden-winged Warblers.

The Bahama Islands have a much poorer fauna than the Antilles, as befits purely oceanic islands, although it is now believed, to quote Shattuck and Miller of the Bahaman expedition of the Geographical Society of Baltimore, that the Bahamas "had undergone a former elevation followed by a more recent depression which in turn had given place to a still later elevation"; but it appears uncertain at present whether the islands are now stationary or undergoing a change of level. As far as the fauna of the Bahamas is concerned, the only mammal found on the islands apart from bats and those introduced by man, is the *Capromys*, a species known only from the eastern island of the French Cays, although it may also be found on the more western French Cay and on Samana Cay. Its nearest relatives are found in Jamaica and on Little Swan Island. The resident Bahaman bird fauna has been chiefly derived from Cuba and Florida, the more distinct and older forms being predominantly Cuban, the Florida element being mostly confined to the northeastern islands. But several Bahaman species are found neither in Cuba nor in Florida. Perhaps the most interesting of these is a genus of Hummingbird, *Nesophlox*, known elsewhere only from Costa Rica and northern Panama. This is evidently a relict genus. A lesser Antillean genus of Thrasher, *Margarops*, also occurs on the more southern and eastern islands of the Bahamas and two wide ranging West Indian genera, *Cæreba* and *Loxigilla*, occur on the islands but do not occur in Cuba or Florida. These are represented practically throughout the West Indies except in Cuba and the Isle of Pines is there represented. The Bahaman *Cæreba* and the Bahaman Tanager of the genus *Spindalis* are said by Riley in an account of the birds of the Bahaman Islands to have been derived from Cozumel Island, Yucatan, where there are closely related forms, but the Tanager certainly has been derived from the Cuban species as has in all probability the Bahaman

Oriole. Two Bahaman birds with interesting distributions are the Bahaman Mockingbird and Thick-billed Vireo. The former species is found elsewhere only on cays off the north coast of Cuba and in Jamaica and its nearest relative is a species found in southeastern Brazil. The Thick-billed Vireo occurs elsewhere only on the island of Tortuga off the north coast of Haiti, an island showing Bahaman affinities both in its plant life and its land mollusks, the Cayman Islands and the Island of Old Providence in the south Caribbean; it is closely related to the North American White-eyed Vireo, closer indeed than it is to any of the other West Indian members of this genus.

To summarize, the West Indies, apart from the Bahama Islands, have a rather small but remarkably rich avifauna with an astonishing number of endemic genera and even two endemic families; that this relict West Indian fauna was probably very like that which existed in northern Central America during the Middle Tertiary period, when the West Indian land area was much larger than it is now and extended much farther to the westward, being probably united at that time with Central America; that Jamaica because of its comparatively rich bird fauna, which shows the greatest proportion of Neotropical species, and because of the presence of the Mosquito Bank which extends some 200 miles northeastward or over one half the distance from Central America to Jamaica, was probably the most recently connected; that the Lesser Antillean Province is very distinct from the Greater Antillean from which it is separated by the Anegada Channel; that from the bird life of the southern Lesser Antilles or British Windward Islands, there is no evidence of a connection with Trinidad although there is every reason to believe that Tobago and Trinidad were once connected; that apart from what is obviously a recent South American element, Neotropical species in the West Indies are very few and almost all the characteristic Neotropical families are entirely lacking; that the avifauna of the West Indian subregion is fundamentally Nearctic and not Neotropical.

CONSERVATION AND EVOLUTION IN A CHANGING SOCIAL PROGRAM

JOHN C. MERRIAM

(Read March 2, 1934)

THE present national emergency has given us relatively high appreciation of three great groups of human problems. The first touches immediate relief of personal suffering and unemployment. A second concerns the devising of means by which dangers to social structure and function can be stayed until new adjustment is made. The third has to do with relation of present specific difficulties to the underlying conditions that determine stability, decadence, and progress of society.

In close relation to large-scale activities directed toward immediate relief of suffering, and operations designed to meet emergency conditions in business, effort is made to guide adjustment of the social program so as to give opportunity for constructive planning. While some see in favorable outcome of the present struggle only a possibility of return to so-called normal times, others accept readjustment as opening the way for progress.

Appreciation of the fact that dangers of the present are due in part to inadequate understanding of many great social questions has brought demand for more knowledge and better vision. In study of major trends in the changing social order, it is clear that one of the principal needs concerns determination of relative values among the almost infinite number of factors involved. For practical purposes of looking ahead on such a great program we should know:

First, what things represent essential and dependable elements upon which we can always build, and which we must therefore conserve or protect.

Second, what tends naturally to change or grow, and may be expected to continue its evolution.

And third, to what extent human constructive or creative ability should contribute toward betterment of conditions.

Discovery of many evils in the institutions and activities of this period has tended to throw the shadow of suspicion over everything. And yet revolutionary overturn might be a more serious menace than existing evils. At such a time, knowledge of what is bad, and what may serve as basis for new building, and what must be looked upon as in a normal state of change, is indispensable, though to obtain it we require the most difficult among all types of judgment.

The enormous extent of detail in existing knowledge makes mastery of the entire range of materials impossible for any individual. Need of specialization in every subject has involved the interests of students to such an extent that few have looked over much of what is available with even approximation to reality. Lack of vision over the broad scope of information already secured is especially regrettable at a period in which it is essential to have somewhere a comprehensive view of science, history, sociology, government, as well as those values which we call spiritual. This situation makes important any useful means of balancing values in terms of their continuing influence.

As point of view is an important element in any discussion, it should be recognized that this paper is written from the position of one trained in science. But dangerous as is exploration by a scientist in the field of human values, it is also true that unless students in scientific subjects join with investigators of human problems to study relations among the several regions of thought, there is small hope for solving some of the questions for which we most urgently need understanding. It should be stated, further, that, in spite of need for specialization, science and the humanities are not separated in the world outside the laboratory. Somewhat as in the long-discussed "conflict of religion and science," the assumed clash between natural science and social science is possible only when there is interference with normal exchange of ideas.

CONSERVATION AND EVOLUTION IN RELATION TO NATURAL
RESOURCES

As seen by the student of natural science, what we call "conservation," "evolution," and the influences of human constructive activity have concrete illustration through our relation to nature and natural resources. In no other field do we have better appreciation of need for understanding what is indispensable to us and requires protection, what must be allowed freedom for natural growth and development, and to what extent human creative activity may bring new values. In no other relation are values of conservation and evolution more clearly measurable in terms of a social program in process of change, or of a future for which we are not yet able to predict a conclusion. Although our relations to natural resources represent only a modest part of that complex group of problems so important in the present social crisis, they happen to constitute critical values in a number of the most significant emergency activities. These relations serve to illustrate point of view regarding conservation and evolution in our changing social program, and to emphasize the need for maintaining proper balance between these elements.

Civilization seems in some measure to have accustomed itself to the idea that, having come into control of new lands, new resources, and the wild places which once dominated the earth, it has in that conquest made the best use of all the benefits to be obtained from this contact. So long as new wildernesses with their virgin resources were still available for discovery and harvest, need of providing against the future was not appreciated. Nor had there come clearly into public consciousness the fact that there *is* a future against which to provide. Today there is realization that we see an end to this store of natural resources. Our desire to protect these possessions is now voiced in the word conservation, with its multitude of interpretations.

Situations similar to that of the present have arisen through all history with reference to natural resources of various

regions as they concerned soil, mines, forests, water and other materials. In numerous ways measures for protection have been devised. But in no earlier period has the world with its resources been mapped out in such manner as to call attention definitely to distinctions between what is replaceable and what is non-replaceable. There has been only partial realization that for some materials there is practically only one supply, made, so to speak, when the earth was formed. Nor was it at first realized that other assets, such as forests, should continue to reproduce themselves, or in one sense that their growth and evolution might continue.

Conservation as the word has been used commonly in this country concerns halting the destruction of resources and certain questions touching ownership brought out in concentration of large public properties under private control. Government moved only slowly to correct abuses which had to do with wasteful or destructive processes. It could and did act more quickly to halt the movement toward concentration of control over great natural resources passing into private hands without adequate return to the people.

In the pioneering stage of this country it was possible to obtain land for farming purposes on comparatively easy terms. The profits were relatively sure, but not great in proportion to the labor expended. In the case of underground mineral wealth, difficulty of locating and testing properties was much larger. Operation was precarious business. At times the returns were of the bonanza type. The element of chance in finding and in realizing on properties made the process in general difficult for all but those prepared to invest relatively large sums in the hope ultimately of obtaining that which could give adequate return on investment.

In some measure the bonanza phase of operation was also to be expected in lumbering operations. Under methods involving harvesting of only one crop from a forest, large properties, large mills, and heavy investment seemed necessary. Methods which gave large returns generally involved also great waste, and frequently left only a bare landscape with little market value.

Rapid harvesting of what were originally the people's resources in natural wealth, along with concentration of these possessions in a limited group of owners, led to protest, to withdrawal of lands, and to modified control of development rights. It led also to better understanding of actual conditions of occurrence and to more careful study of procedure in harvesting.

Had the government many decades ago been able to carry to greater lengths its intensive study of actual conditions from the view of natural science, economic development, and governmental procedure for developing of these natural assets, much waste might have been avoided. Better distribution of wealth would have been possible, and a larger return could have come to the people. A study of history in this field reveals much of interest bearing upon relation between the individual right to discover, acquire, and develop and, on the other side, the public interest and responsibility.

Perhaps the country could afford to have its extraordinary experience in development and waste of natural resources in the period following the Civil War, if from this time on it can profit by the knowledge secured. But it should be clear that while experiences of the next stage of social development will grow out of situations in the past and present, unless the world modifies its habits completely we should expect many further changes in the next stage. These will involve conditions not heretofore recognized. If we are to avoid comparable or more unfortunate situations in the future, in addition to a full understanding of what we should have known and have applied in the past, we shall require much additional information on these subjects from the fields of science, economics, and government.

CONSERVING NON-REPLACEABLE MINERAL WEALTH

Adequate protection of so-called non-replaceable resources requires all possible data regarding their origin, occurrence, manner of synthesis, and means of recovery or harvesting. We should have exhaustive studies on the whole range of uses and possibilities of replacement by more abundant substi-

tutes. Science, economics, and business should join hands in such investigations. For the benefit of posterity, the continuing people should give such support as is not easily furnished by private enterprise.

At the present stage in our study of resources of the non-replaceable type the problem has two outstanding phases: one concerns conservation in the sense of material protection, or guardianship; the other relates to evolution in types of use, and the extent to which human constructive activity can give aid for the future. The nature and degree of protection will be dependent in considerable measure upon the kinds of use. Use depends upon knowledge and desires of the people, and upon their wish to look upon the question as concerning their future.

This discussion thus far has seemed wholly academic, although I believe that it states unequivocal truth, which is never purely academic. What has been said would apply practically in most details to any one of several resources. Oil, or petroleum, illustrates every problem when considered through its history of varying scientific opinions as to origin, nature of occurrence, potential chemical contribution, the adventurous story of its commercial development, of waste, control of ownership, and now of effort for adequate guidance of production through governmental relation. What has been said regarding future possibilities requiring intensive study in every direction also applies fully to this case. That this is recognized is made evident by the wide and deep research on these questions by those most intimately related to industrial development of this group of materials.

MAINTAINING VALUES OF THE SOIL

The soil, the resource upon which man has been most dependent, has of all natural assets seemed the least susceptible to injury. We realize now not only that it suffers seriously through human influence, but that the damage may amount almost to destruction. Without considering what is taken from the ground through unregulated crops, its fertility is

reduced. With no appreciation of influence by tilling and lack of control for wash or drainage, erosion carries away much of its value. In absence of a vegetation cover, exposed areas may be subject to rapid denudation.

Production of a fertile soil may represent ages of preparation by natural process. The work of man can go far to destroy major values within a few years. Wide studies of soil treatment and artificial fertilization have gone far to remedy some of the evils. The major effects of erosion over large areas have been a continuing menace to mankind.

Erosion as a process results from interaction of two groups of natural activities, seen in geological forces expressed as movement of the land and in precipitation, of which neither can be controlled by man. Upward movement of the earth's crust increases the power of running water to wash and cut. This process has been under way through hundreds of millions of years and can be expected to continue for a comparable period.

Regulation of erosion through control of drainage lines and vegetation cover can be planned and guided by man. The influence of unwise tillage, and exposure of areas to increased wash, can be so modified as to limit the detrimental effects.

Based upon thorough study of the factors involved, projects of the government designed to conserve fundamental values of the soil, and to preserve the soil itself, can contribute enormously to conservation of a resource which if seriously impaired can be replaced only with infinite difficulty. In this, as in other cases cited, the need of the moment is for basic knowledge in a wide range of subjects including geological processes and their application to erosion, also soil structure, soil physics and chemistry, climates and meteorology, as also plant cover and its evolution with reference to soil protection.

As in the case of other conservation problems, decisions regarding uses to which the land should be put have great importance. These questions require for their solution an understanding both of evolution in social organization and of

the real desires, purposes, and aspirations of the people concerned.

From another point of view it is important to bear in mind that while the progress of erosion and of soil formation is to be considered as a fundamental or basic phenomenon so far as development of our civilization is involved, it is also true that the process is evolutionary. Crustal movements and erosion processes go forward in cycles, which collectively give us a large part of the story of the earth through recorded geological time. We may adjust ourselves to the stages of these cycles in such manner as to continue use of the soil, but we can not halt the evolutionary development as it advances.

PERMITTING CONTINUING GROWTH AND EVOLUTION OF THE FOREST

Contrasted sharply in most respects with the conservation problem as it touches non-replaceable mineral wealth are the questions involved in use of natural resources of the biological type. Among these features of our environment at the moment outstanding questions are presented by forests and grazing. Of much significance for the future is also the conservation problem relating to wild plants and animals not now in practical economic use.

The executive action of President Cleveland in 1897 which withdrew from private entry large areas of timber land under government ownership was prompted by discovery of rapid destruction of the forests. With subsequent government control harvesting of timber on these areas was carried out according to principles under which the forest was looked upon as a growing, reproducing feature, and not as a single crop to be gathered without reference to the future. The wooded lands came to be considered not merely as a resource of value for the moment, but as something in itself subject to changes the understanding of which is essential to any plan we make for continuing use.

In control of forests, as in administration of non-replaceable resources, it became necessary to obtain knowledge of

every factor concerned. This involved the soils upon which trees grow considered in the light of chemistry, physics, and bacteriology. It was necessary to know the story of climate and of associated plants. It became essential also to have acquaintance with every detail of structure, physiology, reproduction, growth process, and decadent stages of the tree. In ultimate adjustment to this information must come all practices that have to do with harvesting, or in any way touch protection of the soil, or concern the cycles of development in replacement of a forest.

GUARANTEEING PROTECTION AND CONTINUING EVOLUTION OF WILD LIFE

Viewed at one time only as a plaything of the scientist or nature lover, wild plant life not now in economic use may become of critical importance in evolution of society. That the domesticated plants upon which man depends so largely for food, clothing, protection, medication, and many other values constitute all available elements of the plant world that have such value is extremely doubtful.

The plant species at present in use were obtained by ancient peoples through ages of contact. Attention was centered on cultivation and betterment of these materials. Either emergency conditions or intensive research will bring out still other species having hitherto unrecognized values.

During the Great War, when we were in search for rubber supply, it was estimated that one billion pounds of rubber could be obtained from the rabbit brush of the arid region in and bordering Nevada. Perhaps future studies of land use will make desirable some development of this resource through bettered strains of this and similar plants in regions where other agricultural ventures are less profitable.

One may expect that in future ages scientific discovery will give us yet undreamed methods for modification of the plant world to meet new human needs. But it is highly improbable that such researches will furnish us a range of new species comparable to those now found in the wild flora that

has been produced through hundreds of millions of years of evolution in the environment of a constantly changing earth. It is essential that guardianship of such relics as we have be maintained, and that careful research be directed toward study of possible resources for the future.

So again in wild animal life, the great resource of game animals and other creatures remaining in the wild state deserves our protection for possibilities represented in a multitude of uses. These range from food, recreation, and stimulating experience of the hunter, to interest in such life for its own sake that serves an increasingly important purpose as opportunity develops for us to turn again toward the values of nature.

CONSERVATION OF GREAT NATURAL FEATURES IN THEIR PRIMITIVE CONDITION

One of the most difficult, and yet in some ways one of the most important functions of conservation at this time, looks in still another direction toward preservation and protection of those overshadowing features of nature which illustrate both the processes and the results that have contributed toward shaping the world as we find it. Such aspects of our surroundings appear in the power of natural forces, in the primitive life which has grown out of the creative process, and in great landscapes comprising the whole range of features in nature.

The values maintained in this type of conservation or protection, and the uses toward which they contribute, comprise an infinite variety of things relating to aspects of life which concern our maintenance through food, shelter, control of power, and knowledge of the entire range of natural resources. In at least equally important ways they meet needs touching the things that are most strikingly characteristic of man, namely, his intellectual growth, his appreciation of beauty and sublimity in nature, and the desire to adjust his spiritual or religious life to what is known of creative influences in the world about us.

It is a part of the task of science to make acquaintance with the elements of our natural surroundings. Nature is almost infinitely complex, and to know it adequately we must study its operations without the disturbing or complicating influence of artificial factors. So from time to time areas which present exceptional features have been set aside for complete protection.

The manner in which various human uses may be intertwined in such possessions is illustrated in simple manner by the sacred forests surrounding ancient temples in China. These wooded areas seem to have been maintained partly to give protection to the temples, partly by reason of their beauty as frames for these structures, but largely because they were places in which it was possible to walk in quiet natural surroundings and to meditate on great questions of life and religion. This desire for contemplation in the midst of undisturbed natural beauty, which made the preservation of these wooded areas possible, has brought most interesting results.

Dr. Lowdermilk, of the federal Soil Erosion Service, a close student of problems in China, tells me that the sacred forests are almost the only places in those regions where the natural features have been left undisturbed. It is here that he found opportunity to compare the original face of the land with the heavily eroded areas of today. It is in such forests alone that the beautiful maiden-hair, or ginkgo, tree, which was once spread widely over the northern hemisphere, remains now for our use and study. It is here that, in the desire to maintain nature as nearly as possible in its original condition, certain areas, that have been used in some part to meet needs of the community, have long been treated by methods of forest conservation corresponding to what we are at this moment initiating as a national practice of the United States through the timber conservation policy.

Protection of great features of nature which illustrate outstanding results of creation, or of the processes by which this work has been accomplished, is especially important when what is guarded remains in its primeval environment. Only

with such conditions can we have real appreciation of nature at work, and of the conditions under which its activity proceeds.

CONSERVATION OF NATURAL BEAUTY

In addition to what might be called the creational values of nature which we may protect for future students, scientific, intellectual, and economic, strong emphasis should be placed on that significant phase of conservation covering the diverse elements which human appreciation groups under the head of beauty in nature. On the assumption that beauty represents only an attitude of mind toward harmonious values, we must recognize this point of view as connected with that relating to the element of the sublime in nature expressing respect for things of magnitude and power. Though beauty may be dependent upon how we look, or the point of view which we take, the elements combined to form the picture of beauty and sublimity must be conceived as existing in nature and not wholly due to human imagination.

So conservation as it touches nature should cover features representing beauty and sublimity and the great group of influences which inspire us. Through this guardianship we protect materials that serve as the source from which may develop critical elements not only of scientific thought, but of æsthetic ideals, or even ideas of significance in growth of religious thought.

NECESSITY FOR EVOLUTION OF HIGHEST ATTAINABLE STANDARDS OF USE FOR GREAT TREASURES IN NATURE

Building of the National Park system of the United States offers one of the exceptional possibilities for preserving features in nature recognized as superlative from points of view ranging through economic and scientific to the æsthetic, poetic, and religious. Maintenance of these values as they have been transmitted to us, and guidance of their use for scientific, intellectual, and spiritual purposes constitutes one of the unique responsibilities of the world.

Proper development of the opportunity furnished for study of creation, its processes, and the relation of man to it will require a synthesis of all that we possess in science, in art, and in philosophy. The result will conceivably furnish a new aspect of intellectual and spiritual interest having large significance in the future development of our beliefs regarding the relation of man to nature. It will be an outstanding influence both in conservation of ideas and in evolution of ideals. So important may this contribution be to a world of changing and developing views that no effort should be spared to maintain the treasures set aside for this purpose. It is important to realize that adequacy of protection depends upon ability so to define the values and manner of use for what is involved that unwitting destruction will be avoided.

CONSERVATION AND EVOLUTION IN THE FIELD OF HUMAN ACTIVITIES

In the region of nature we have come to an appreciation of our responsibilities for protection of basic resources, and for continuing study of their utilization in such manner as to meet requirements in the evolution of our highest needs. We do not understand the balance of these functions fully, but we appreciate the significance of the problem.

Within the special domain of human problems, determination of what requires conservation, what concerns evolution or development, and what is clearly the peculiar opportunity for man's constructive ability is more difficult than in examination of our relation to nature. There are nevertheless in the phenomena of life, whether considered as biological or in terms of human thought, certain things which the tests of time and experience show to be fundamental. In other aspects of life we find expectation of change and development or growth inherent in the situation. And again there are conditions in which the stage seems set specifically as opportunity for human creative activity. The possibility of orderly movement in social development depends in considerable measure upon our ability to determine the balance which

should obtain among these factors. This is one of the greatest of all human questions.

The view that there are *no* basic or fundamental qualities means a situation in which changes will be largely dependent upon the momentary whims of individuals or groups. In common language this is chaos. On the other hand, inflexible adherence to the idea that *nothing* changes results in attempt to tie down the growing structure of society. The result is that sooner or later the bonds are rudely broken. Appreciation of the idea that society *desires* opportunity for *progress* opens the way for those processes of growth by which changes, sometimes slow and sometimes rapid, bring about normal evolution.

The known history of the world permits us to visualize the entrance of man into the scheme of things at some remote period, and to see him bringing a new constructive element. The coming of this influence gave added possibilities for organizing and storing knowledge, and finally for selective judgment. Whether one looks upon the appearance of human kind as only another expression of the Creator, or however it be interpreted, with its coming a further type of vision opened in the world. With increasing knowledge of nature and of man himself, previously unknown combinations were made possible, and under these conditions forward building was to be expected in all later stages.

OPPORTUNITY FOR CONSERVATION AND EVOLUTION IN ABORIGINAL AMERICAN CULTURE

In human application of conservation and evolution principles derived from study of nature, we find illustration of an activity having much significance today in a program under discussion for widening opportunities of life for the native or Indian peoples of this country. With differing views as to how this may be accomplished, consideration is being given to adjustment such as can guarantee to the Indian the possibility of following as he may wish the ideas or ideals which his nature or his culture indicates as most desirable.

Of the courses which can be followed one possibility looks toward early amalgamation of all the peoples of the country, and possible assumption of characteristics like those distinguishing the Anglo Saxon people. From another point of view, there would be recognized in human nature an assortment of qualities which are in part expression of individual peculiarities, but in large measure represent more fundamental strata corresponding to influence of inheritance and environment.

This particular problem concerns extent to which the aboriginal American may be given opportunity to develop on the basis of conservation of his fundamental characters, inclinations, and ideals. It involves also the extent to which in his evolution he should have aid in accommodating himself so far as he may desire to the conventions of European civilization. It has taken the cultural groups of Europe many generations to attain appreciation of the fact that the things which appear good to one nation, or in one culture, may not have comparable value to those representing development out of a different environment, and on the basis of different ideals. The world is still seeking for light as to how such problems should be solved.

SIGNIFICANCE OF CONSERVATION AND EVOLUTION IN PRACTICAL QUESTIONS OF SOCIETY TODAY

When we turn to application of conservation and evolution principles as they relate to the particular problems of our civilization in this period of depression one can not avoid recognizing first of all the seemingly infinite extent and complication of forces in action. The picture is today so vast, and the factors concerned so little understood, that the problem is impressive by reason of almost incomprehensible magnitudes and through recognition of our ignorance. The tremendous difficulties of the situation make it more clear at the present time than at any earlier moment in history that, within reasonable limits, we must determine what among the elements of science, economics, government, and religion

appear to be firm ground upon which we can build, also what must be looked upon as in normal change or progress. And again we see that it is important to recognize those situations in which failure to act constructively might be tantamount to neglect of responsibility.

With what may be called the modern fact-finding view, we appreciate that determination of what is basic and of continuing value and what is of progressive or evolutionary type can be determined only by intensive examination of the facts. In this effort the combination of science and history with consideration of moral and ethical values becomes important far beyond the degree of acquaintance with this relation in any previous age. We have too often considered as practical only the things of immediate or personal significance. In reality practical values involve a wider vision concerning the highest truth and greatest good over the longer period.

While the principles of conservation and evolution can not be expected to apply to the affairs of man in precisely the manner in which we see them related to factors in nature, they are as clearly fundamental as in the remainder of the created world. This may be illustrated by the fact that in this country our political organization rests practically upon a two-party system consisting of a conservative and a liberal group. In general, one body stands more especially for conservation and development of certain great fundamental ideas or practices. The other inclines toward freedom of action and to introduction of new elements. As political bodies they may almost completely exchange places, but the distinguishing principle remains.

In another direction it is interesting to note that just as we have studied conservation of natural resources with reference to values involved in ownership, and in control, and have taken measures so to regulate conditions as to give better protection of values and wider liberty of opportunity to the public, so at this moment we are deeply concerned with what might be called the bonanza aspect of money-making illustrated by forms of high finance. Great fortunes of the

bonanza type derived from natural resources seemed in the past too frequently to represent private control of what had been derived from public ownership, with inadequate return to the people. Today we are concerned over possibilities of financial control which might permit gathering of large fortunes by methods not clearly representing true earning power.

Study of means by which activities permitting great concentrations of wealth may be guided look toward protection of something which arises in large part from constructive activity of the whole people. The concentration of money power of the nation in the hands of a small group might center control of other activities, including educational and intellectual opportunity, or even guidance of ideas. The process involved in conserving freedom for action is in some respects not unrelated to conservation activities developed in relation to natural resources.

We find in this age vigorous effort to eliminate poverty and secure opportunity for education and the broader view for all citizens. With this are coupled in some measure the activities designed to prevent great concentration of wealth by opening better means for its distribution. These questions are all related to fundamental principles concerning right of the individual to live his own life and grow in proportion to his capacity for development. This condition has been described through the ages in many ways and in numerous languages. It has been called liberty, or opportunity, or the pursuit of happiness. It rests upon ideas of life and government that involve both individual opportunity and responsibility to the community. The principles of truth, honesty, and brotherly love have worked themselves out slowly in relation to these aspects of control in possession of property, in general human relations, and in government. They lie in a stratum deeper than laws or codes. It is the spirit of conduct and not the letter of laws that determines truth, honesty, and broadly all human values.

Much of the struggle in which we are engaged at the moment in this country, and in the world, ranges within the

limits of the few principles or questions discussed. The conservation and continuing high use of great human ideals demonstrated over and over in history, but abundantly neglected in practice, is one of the most critical needs of this time. Standards of conduct are more fundamental than any other bases of reference. There is properly and necessarily strenuous discussion regarding intricate questions of economic and social organization, and this must all be given full consideration and much research. But in proportion to values involved, it sometimes seems as if there is less said about the fundamental principles underlying right conduct of business and of human relations, individual, national, and international, than of immediate technical details that represent evolution of our social structure. We have just spent many painful years considering individual liberty as it touches constitutional rights involved in prohibition legislation. In the meantime the cause of temperance has at times appeared less important than the right to drink.

EVOLUTION OF CREATIVE ACTIVITY IN RELATION TO WELFARE OF SOCIETY

In considering more especially those features of present-day life that have to do with evolution of society and expression of human creative activity, science in its varying forms has been given a prominent place. Few other types of activity have been looked upon as having so large a responsibility for present lack of social adjustment. It is not that science has been considered in itself evil or destructive, but rather that through its advance there has come into the world an almost infinite number of new forces, methods, and instruments causing tremendously rapid development in certain directions as compared with limited possibilities in others. The resulting unbalance has appeared to affect all aspect of human thought and activity. In a period of depression this relation takes on special importance.

Question has naturally arisen as to the attitude we should take toward these elements which tend to promote exceptionally rapid evolution in civilization, or in another view

might be looked upon as over-emphasis on human creative activity. While this development has been most strongly expressed in the physical sciences, no phase of thinking, from physics to social theory, has failed to exert its influence through production of new materials.

In the great mass of new information contributed by this constructive work the product is such that under proper conditions of control it would be recognized as having large value. It is principally those things which are advanced or promoted without reference to their wider or ultimate human significance that come to be looked upon as detrimental. This may be true of forms of energy, mechanical inventions, chemical substances, drugs, aspects of art and literature, or theories of social organization.

We can not doubt that from time to time discovery and invention have brought difficult social disturbance. The results are not unlike numerous known cases in which plants or animals have been moved into a region not adjusted to their presence, and have disturbed the balance of nature. Such is the story of the cactus, or of rabbits brought into the Australian region, where such types of organisms had not existed in this or any preceding period. At the same time there seems no question that with adequate vision these new products or advances in knowledge collectively are of benefit to mankind. They present possibilities for adjustment on new levels, and with widened opportunities for life.

The control of new features will in many instances require a view such as can be obtained only by wisdom of the highest order. Perhaps we shall need the collective judgment of many minds related in an exceptionally effective way. In other cases the necessary action may arise from individuals concerned. To depend wholly upon values remaining through survival of the fittest, allowing things to take their course unguided, will sometimes involve fate of the product and on other occasions the interests of the people. Errors of ignorance in handling of such situations will be multiplied by bad judgment, and may be increased almost infinitely by selfishness or neglect of the public interest.

In ways not yet devised we need development of research, education, and vision which will give us machinery making possible the continuing evolution of society through creative activity, but without increasing the dangers. Such a program will necessarily involve participation of science and engineering in its various phases, along with representation of all social interests concerned.

Desire and ability to increase knowledge and extend creative work are normal and essential characters of an intelligent people. To halt such activities would be to limit that forward movement which is indispensable in a world of people whose happiness is in large part determined by their opportunities for progress.

We have adequate knowledge from history to indicate that we live in a changing or evolving world, and this need not now be disputed or argued. We know also that adequate development through the varying stages of life depends upon the working out of great principles and ideas. As the movement continues we must retain and conserve the things which are fundamental and at the same time give liberal room for changing elements, with normal evolution and creative activity such as enter at every age. With this continuing development there is no problem more important than that of maintaining balanced judgment and means of adjustment adequate to progress with the minimum of loss and the maximum of value for constructive effort.

Let us not be deceived into setting up an alibi through thinking that science has disturbed the values of truth, or that real business necessarily makes exchange and barter unholy, or that natural passion and art demean the spirit of man. Perhaps in application of principles of conservation and evolution to human affairs we need the voice of the preacher along with that of the scientist, engineer, economist, and student of government to tell us whether the scales of our judgment are properly adjusted. If such balance can be maintained as will give true appraisal of relations between major values, the way for progress will be seen as a wide and pleasant road.



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Members admitted:

Gilbert Chinard
 William H. Collins
 William B. Dinsmore
 Edward V. Huntington
 Lewis R. Jones
 Charles A. Kofoid
 Burton E. Livingston
 John R. Marlin
 Marshall S. Morgan
 Francis R. Packard
 Henry A. Sanders
 Samuel P. Wetherill

deceased:

Arthur P. Davis
 William M. Davis
 Alfred F. Hess
 Archibald B. Macallum
 George O. Squier
 Augustus Trowbridge

elected:

Detlev W. Bronk
 Willa Cather
 Gustavus W. Cook
 Wilber L. Cross
 Cass Gilbert
 Edward S. Harkness
 Horace H. F. Jayne
 Alfred V. Kidder
 John L. Lowes
 Frederick Novy
 Conyers Read
 Jesse S. Reeves
 Owen J. Roberts
 George Sartori
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ERRATUM

For:

Benjamin Franklin, January 2, 1789 – d. April 17, 1790.

Read:

Benjamin Franklin, January 2, 1769 – d. April 17, 1790.

OFFICERS

PRESIDENTS

Benjamin Franklin, January 2, 1789 - d. April 17, 1790.
 David Rittenhouse, January 7, 1791 - d. June 26, 1796.
 Thomas Jefferson, January 6, 1797 - resigned, November 23, 1814.
 Caspar Wistar, January 6, 1815 - d. January 22, 1818.
 Robert Patterson, January 1, 1819 - d. July 22, 1824.
 William Tilghman, January 7, 1825 - d. April 29, 1827.
 Peter Stephen Du Ponceau, January 4, 1828 - d. April 1, 1844.
 Robert M. Patterson, January 3, 1845 - declined accepting position.
 Nathaniel Chapman, January 2, 1846 - January 5, 1849.
 Robert M. Patterson, January 5, 1849 - January 7, 1853.
 Franklin Bache, January 7, 1853 - January 5, 1855.
 Alexander Dallas Bache, January 5, 1855 - January 2, 1857.
 John K. Kane, January 2, 1857 - d. February 21, 1858.
 George B. Wood, January 7, 1859 - d. March 30, 1879.
 Frederick Fraley, January 2, 1880 - d. September 23, 1901.
 Isaac J. Wistar, January 3, 1902 - January 2, 1903.
 Edgar F. Smith, January 2, 1903 - January 3, 1908.
 William W. Keen, January 3, 1908 - January 4, 1918.
 William B. Scott, January 4, 1918 - April 25, 1925.
 Charles D. Walcott, April 25, 1925 - d. February 9, 1927.
 Francis X. Dercum, April 28, 1927 - d. April 23, 1931.
 Henry Norris Russell, December 4, 1931 - April 22, 1932.
 Roland S. Morris, April 22, 1932 -

VICE-PRESIDENTS

1769

Thomas Cadwalader
 Thomas Bond
 Joseph Galloway

1776

Thomas Bond
 Samuel Rhoads
 William Smith

1770 to 1775, inclusive

Joseph Galloway
 Thomas Bond
 Samuel Rhoads

(No minutes from January 5,
 1776 to January 16, 1779)

1779

Thomas Bond
David Rittenhouse
William Shippen

(No minutes for 1780)

1781 and 1782

Thomas Bond
David Rittenhouse
James Wilson

1783 and 1784

William White
Thomas Bond
John Ewing

1785 and 1786

John Ewing
William White
Samuel Vaughan

1787 to 1789, inclusive

John Ewing
William White
David Rittenhouse

1790

John Ewing
David Rittenhouse
William Smith

1791 to 1794, inclusive

John Ewing
William Smith
Thomas Jefferson

1795

Nicholas Collin
Thomas Ruston
Caspar Wistar

1796

Nicholas Collin
William Smith
Caspar Wistar

1797 and 1798

Caspar Wistar
Benjamin Rush
Nicholas Collin

1799 and 1800

Caspar Wistar
Benjamin Rush
Robert Patterson

1801

Caspar Wistar
Robert Patterson
Andrew Ellicott

1802 to 1814, inclusive

Robert Patterson
Caspar Wistar
Benjamin Smith Barton

1815

Robert Patterson
Benjamin Smith Barton
Jonathan Williams, Jr.

1816 to 1818, inclusive

Robert Patterson
William Tilghman
Peter Stephen Du Ponceau

1819 to 1824, inclusive

William Tilghman
Peter Stephen Du Ponceau
Zaccheus Collins

1825 to 1827, inclusive

Peter Stephen Du Ponceau
Zaccheus Collins
Robert M. Patterson

1828 and 1829

Zaccheus Collins
Robert M. Patterson
Nathaniel Chapman

(No minutes for 1830)

1831.

Zaccheus Collins
Nathaniel Chapman
Joseph Hopkinson

1832 to 1835, inclusive
Nathaniel Chapman
Joseph Hopkinson
George Ord

1836 to 1842, inclusive
Nathaniel Chapman
Joseph Hopkinson
Robert M. Patterson

1843 and 1844
Nathaniel Chapman
Robert M. Patterson
Franklin Bache

1845
Franklin Bache
Alexander Dallas Bache
Nathaniel Chapman

1846 to 1848, inclusive
Robert M. Patterson
Franklin Bache
Alexander Dallas Bache

1849 to 1852, inclusive
Franklin Bache
Alexander Dallas Bache
John K. Kane

1853 and 1854
Alexander Dallas Bache
John K. Kane
Robley Dunglison

1855 and 1856
John K. Kane
Robley Dunglison
John F. Frazer

1857

Robley Dunglison
John F. Frazer
John C. Cresson

1858

Robley Dunglison
John C. Cresson
Isaac Lea

1859 to 1868, inclusive

John C. Cresson
Isaac Lea
George Sharswood

1869 to 1876, inclusive

John C. Cresson
Isaac Lea
Frederick Fraley

1877 to 1879, inclusive

Frederick Fraley
Eli K. Price
E. Otis Kendall

1880 to 1883, inclusive

Eli K. Price
E. Otis Kendall
John L. Le Conte

1884

Eli K. Price
E. Otis Kendall
Pliny E. Chase

1885 and 1886

E. Otis Kendall
Pliny E. Chase
W. S. W. Ruschenberger

1887 to 1895, inclusive

E. Otis Kendall
W. S. W. Ruschenberger
J. Peter Lesley

- 1896 and 1897
E. Otis Kendall
J. Peter Lesley
William Pepper
- 1898
E. Otis Kendall
William Pepper
Coleman Sellers
- 1899 to 1902, inclusive
Coleman Sellers
Isaac J. Wistar
George F. Barker
- 1903 and 1904
George F. Barker
Samuel P. Langley
William B. Scott
- 1905 to 1908, inclusive
George F. Barker
William B. Scott
Simon Newcomb
- 1909
William B. Scott
Simon Newcomb
Albert A. Michelson
- 1910 to 1916, inclusive
William B. Scott
Albert A. Michelson
Edward C. Pickering
- 1917
William B. Scott
Albert A. Michelson
George Ellery Hale
- 1918
Albert A. Michelson
- George Ellery Hale
Joseph G. Rosengarten
- 1919 to 1921, inclusive
George Ellery Hale
Arthur A. Noyes
Hampton L. Carson
- 1922
Arthur A. Noyes
Henry Fairfield Osborn
Hampton L. Carson
- 1923 and 1924
Hampton L. Carson
Henry Fairfield Osborn
William W. Campbell
- 1925 and 1926
Henry Fairfield Osborn
William W. Campbell
Francis X. Dercum
- 1927
Henry Fairfield Osborn
William W. Campbell
James H. Breasted
- 1928 and 1929
William W. Campbell
James H. Breasted
Elihu Thomson
- 1930 and 1931
James H. Breasted
Elihu Thomson
Henry Norris Russell
- 1932
James H. Breasted
Elihu Thomson
Edwin G. Conklin

OFFICERS

375

1933

Elihu Thomson
Edwin G. Conklin
Alba B. Johnson

1934

Edwin G. Conklin
Alba B. Johnson
Robert A. Millikan

SECRETARIES

1769

Charles Thomson
William Smith
Thomas Mifflin
John Ewing

1776

Robert Strettell Jones
Benjamin Rush
Richard Wells
Thomas Bond, Jr.

1770

William Smith
Charles Thomson
Thomas Mifflin
S. Roberts

(No minutes from January 5,
1776 to January 16, 1779)

1779

William Smith
John Ewing
William White
Owen Biddle

1771

William Smith
David Rittenhouse
John Ewing
Robert Strettell Jones

(No minutes for 1780)

1772

William Smith
Robert Strettell Jones
William Shippen, Jr.
Charles Moore

1781

John Ewing
Owen Biddle
Timothy Matlack
William White

1773

William Smith
Robert Strettell Jones
Owen Biddle
Benjamin Rush

1782

John Ewing
William White
James Hutchinson
Timothy Matlack

1774 and 1775

William Smith
Richard Wells
Robert Strettell Jones,
Benjamin Rush

1783

James Hutchinson
Hugh Shiell
James Davidson
Timothy Matlack

1784

Robert Patterson
James Hutchinson
Thomas Bond, Jr.
John C. Kunzie

1785

James Hutchinson
Thomas Bond, Jr.
Robert Patterson
Samuel Magaw

1786 to 1788, inclusive

James Hutchinson
Samuel Magaw
Robert Patterson
John Foulke

1789 and 1790

James Hutchinson
Robert Patterson
Samuel Magaw
John Vaughan

1791 to 1793, inclusive

James Hutchinson
Robert Patterson
Jonathan Williams, Jr.
Samuel Magaw

1794

Nicholas Collin
William Barton
Robert Patterson
Samuel Magaw

1795 and 1796

William Barton
John Bleakley
Samuel Magaw
Robert Patterson

1797

William Barton
John Bleakley
Samuel Magaw
Jonathan Williams, Jr.

1798

Samuel Magaw
Adam Seybert
Thomas C. James
Samuel H. Smith

1799

Thomas C. James
Samuel H. Smith
Adam Seybert
James Woodhouse

1800

Adam Seybert
Joseph Clay
Samuel H. Smith
Thomas Peters Smith

1801

John Redman Coxé
Adam Seybert
Joseph Clay
Burgess Allison

1802

Joseph Clay
John Redman Coxé
Thomas C. James
Adam Seybert

1803 to 1807, inclusive

Adam Seybert
John Redman Coxé
Thomas C. James
Thomas Tickell Hewson

1808

Thomas C. James
Adam Seybert
Thomas Tickell Hewson
Nathaniel Chapman

1809

Thomas C. James
Thomas Tickell Hewson
Nathaniel Chapman
Mahlon Dickerson

1810 and 1811

Thomas C. James
Thomas Tickell Hewson
Nathaniel Chapman
Burgess Allison

1812

Thomas C. James
Thomas Tickell Hewson
Nathaniel Chapman
Joseph Cloud

1813

Thomas C. James
Thomas Tickell Hewson
Nathaniel Chapman
Robert M. Patterson

1814

Thomas C. James
Thomas Tickell Hewson
Robert M. Patterson
Reuben Haines

1815 and 1816

Thomas C. James
Thomas Tickell Hewson
Robert M. Patterson
Nathaniel Chapman

1817 and 1818

Thomas C. James
Robert M. Patterson
John Syng Dorsey
W. P. C. Barton

1819

Thomas C. James
Robert M. Patterson
W. P. C. Barton
Robert Walsh, Jr.

1820

Thomas C. James
Robert M. Patterson
Robert Walsh, Jr.
George Ord

1821 and 1822

Thomas Tickell Hewson
Robert M. Patterson
Robert Walsh, Jr.
George Ord

1823 and 1824

Robert M. Patterson
Robert Walsh, Jr.
George Ord
William H. Keating

1825 and 1826

Robert Walsh, Jr.
George Ord
William H. Keating
Franklin Bache

1827

George Ord
William H. Keating
Franklin Bache
Clement C. Biddle

1828

Franklin Bache
Clement C. Biddle
John K. Kane
Charles D. Meigs

1829

George Ord
Franklin Bache
Clement C. Biddle
John K. Kane

(No minutes for 1830)

1831

George Ord
Franklin Bache
Clement C. Biddle
John K. Kane

1832

Franklin Bache
Clement C. Biddle
John K. Kane
William H. Keating

1833 to 1837, inclusive

Franklin Bache
John K. Kane
Alexander Dallas Bache
Charles D. Meigs

1838 and 1839

Franklin Bache
John K. Kane
Alexander Dallas Bache
Joshua Francis Fisher

1840 to 1842, inclusive

Franklin Bache
John K. Kane
Alexander Dallas Bache
Robley Dunglison

1843 and 1844

John K. Kane
Alexander Dallas Bache
Robley Dunglison
Joshua Francis Fisher

1845 to 1847, inclusive

John K. Kane
Robley Dunglison
John F. Frazer
Alfred Langdon Elwyn

1848

John K. Kane
Robley Dunglison
John F. Frazer
Charles B. Trego

1849 to 1852, inclusive

Robley Dunglison
John F. Frazer
Charles B. Trego
E. Otis Kendall

1853 and 1854

John F. Frazer
Charles B. Trego
E. Otis Kendall
Frederick Fraley

1855 to 1858, inclusive

Charles B. Trego
E. Otis Kendall
Frederick Fraley
John L. Le Conte

1859 to 1874, inclusive

Charles B. Trego
E. Otis Kendall
John L. Le Conte
J. Peter Lesley

OFFICERS

379

1875 and 1876

E. Otis Kendall
John L. Le Conte
Pliny E. Chase
J. Peter Lesley

1877 to 1879, inclusive

John L. Le Conte
Pliny E. Chase
George F. Barker
J. Peter Lesley

1880 to 1883, inclusive

Pliny E. Chase
George F. Barker
J. Peter Lesley
Daniel G. Brinton

1884 to 1886, inclusive

George F. Barker
Daniel G. Brinton
Henry Phillips, Jr.
J. Peter Lesley

1887 to 1895, inclusive

George F. Barker
Daniel G. Brinton
Henry Phillips, Jr.
George H. Horn

1896

George F. Barker
George H. Horn
Persifor Frazer, Jr.
Patterson Du Bois

1897

George H. Horn
Persifor Frazer, Jr.
Isaac Minis Hays
Frederick Prime

1898

Persifor Frazer, Jr.
Isaac Minis Hays
Frederick Prime
Samuel Philip Sadtler

1899 and 1900

Isaac Minis Hays
Frederick Prime
Samuel Philip Sadtler
Richard A. Cleemann

1901

Isaac Minis Hays
Samuel Philip Sadtler
Edwin G. Conklin
Arthur W. Goodspeed

1902 to 1907, inclusive

Isaac Minis Hays
Edwin G. Conklin
Arthur W. Goodspeed
Morris Jastrow, Jr.

1908 to 1911, inclusive

Isaac Minis Hays
Arthur W. Goodspeed
James W. Holland
Amos P. Brown

1912 to 1917, inclusive

Isaac Minis Hays
Arthur W. Goodspeed
Amos P. Brown
Harry F. Keller

1918 and 1919

Isaac Minis Hays
Arthur W. Goodspeed
Harry F. Keller
Bradley Moore Davis

OFFICERS

1920 and 1921

Isaac Minis Hays
 Arthur W. Goodspeed
 Harry F. Keller
 John A. Miller

1922 and 1923

Arthur W. Goodspeed
 Harry F. Keller
 John A. Miller

1924 to 1934, inclusive

Arthur W. Goodspeed
 John A. Miller

CURATORS

1769

Adam Kuhn
 John Morgan
 Lewis Nicola

1770

Isaac Bartram
 Benjamin Rush
 Owen Biddle

1771

William Shippen, Jr.
 Benjamin Rush
 Adam Kuhn

1772

Benjamin Rush
 James Alexander
 David Rittenhouse

1773

David Rittenhouse
 Samuel Duffield
 James Alexander

1774 and 1775

Samuel Duffield
 David Rittenhouse
 Thomas Bond, Jr.

1776

David Rittenhouse
 Samuel Duffield
 Pierre E. Du Simitiere

(No minutes from January 5,
 1776 to January 16, 1779)

1779

Lewis Nicola
 Samuel Duffield
 Pierre E. Du Simitiere

(No minutes for 1780)

1781

Lewis Nicola
 Samuel Duffield
 Pierre E. Du Simitiere

1782

Lewis Nicola
 Samuel Duffield
 Isaac Gray

1783

Samuel Duffield
 Isaac Gray
 Ebenezer Hazard

1784 and 1785

Ebenezer Hazard
 Samuel Duffield
 Lewis Nicola

1786 and 1787

Samuel Duffield
 Barnabas Binney
 William Bradford

1788 and 1789

Samuel Duffield
William Bradford
Charles W. Peale

1790 and 1791

Samuel Duffield
Charles W. Peale
Benjamin Smith Barton

1792 to 1794, inclusive

Charles W. Peale
Benjamin Smith Barton
Caspar Wistar

1795 and 1796

Benjamin Smith Barton
Thomas Parke
Charles W. Peale

1797 and 1798

Charles W. Peale
Benjamin Smith Barton
Robert Patterson

1799

Charles W. Peale
Benjamin Smith Barton
Nicholas Collin

1800

Charles W. Peale
Benjamin Smith Barton
George Turner

1801 and 1802

Charles W. Peale
Robert Leslie
John R. Smith

1803

Charles W. Peale
Robert Leslie
William S. Jacobs

1804 to 1806, inclusive

Charles W. Peale
Robert Hare, Jr.
John Church

1807 to 1810, inclusive

Charles W. Peale
Robert Hare, Jr.
John R. Smith

1811 to 1813, inclusive

John R. Smith
Zaccheus Collins
Robert Hare, Jr.

1814 and 1815

Zaccheus Collins
Joseph Cloud
William Hembel, Jr.

1816

Zaccheus Collins
Joseph Cloud
Samuel Calhoun

1817 and 1818

Zaccheus Collins
Joseph Cloud
Thomas Tickell Hewson

1819 and 1820

Joseph Cloud
Thomas Tickell Hewson
Reuben Haines

1821 and 1822

Joseph Cloud
Thomas Say
William E. Horner

1823

Thomas Say
William E. Horner
Isaiah Lukens

- | | |
|-------------------------|-------------------------|
| 1824 to 1827, inclusive | 1857 and 1858 |
| Thomas Say | Franklin Peale |
| William E. Horner | Elias Durand |
| James Mease | M. Fisher Longstreth |
| 1828 | 1859 to 1870, inclusive |
| James Mease | Franklin Peale |
| William E. Horner | Elias Durand |
| John Price Wetherill | Joseph Carson |
| 1829 | 1871 to 1873, inclusive |
| James Mease | Joseph Carson |
| John Price Wetherill | Elias Durand |
| Robert E. Griffith, Jr. | Hector Tyndale |
| (No minutes for 1830) | 1874 to 1876, inclusive |
| 1831 to 1836, inclusive | Joseph Carson |
| Robert E. Griffith, Jr. | Hector Tyndale |
| John Price Wetherill | Charles M. Cresson |
| Isaac Lea | 1877 to 1879, inclusive |
| 1837 | Hector Tyndale |
| Isaac Lea | Charles M. Cresson |
| John Price Wetherill | Daniel G. Brinton |
| Isaac Hays | 1880 |
| 1838 | Hector Tyndale |
| Isaac Lea | Charles M. Cresson |
| Isaac Hays | Henry Phillips, Jr. |
| Franklin Peale | 1881 to 1883, inclusive |
| 1839 to 1845, inclusive | Charles M. Cresson |
| John Price Wetherill | Henry Phillips, Jr. |
| Isaac Hays | George H. Horn |
| Franklin Peale | 1884 and 1885 |
| 1846 to 1850, inclusive | George H. Horn |
| Franklin Peale | Charles G. Ames |
| John Price Wetherill | Philip H. Law |
| John C. Cresson | 1886 |
| 1851 to 1856, inclusive | George H. Horn |
| Franklin Peale | Charles G. Ames |
| John C. Cresson | John R. Baker |
| M. Fisher Longstreth | |

1887 and 1888	William P. Wilson
Charles G. Ames	William B. Scott
John R. Baker	
Philip H. Law	1903 to 1907, inclusive
	Charles L. Doolittle
1889 and 1890	William P. Wilson
John R. Baker	Albert H. Smyth
Patterson Du Bois	
J. Cheston Morris	1908 to 1919, inclusive
	Charles L. Doolittle
1891 to 1895, inclusive	William P. Wilson
Patterson Du Bois	Leslie W. Miller
J. Cheston Morris	
Richard Meade Bache	1920 and 1921
	William P. Wilson
1896	Leslie W. Miller
J. Cheston Morris	Henry H. Donaldson
Richard Meade Bache	
Benjamin Smith Lyman	1922
	William P. Wilson
1897 to 1901, inclusive	Henry H. Donaldson
J. Cheston Morris	
Benjamin Smith Lyman	1923 to 1927, inclusive
Henry Pettit	William P. Wilson
1902	1928 to 1934, inclusive
Charles L. Doolittle	Albert P. Brubaker

TREASURERS

1769 and 1770	1791 to 1841, inclusive
Philip Syng	John Vaughan
1771 to 1776, inclusive	1842 to 1847, inclusive
Thomas Coombe	George Ord
(No minutes from January 5, 1776 to January 16, 1779)	1848 to 1851, inclusive
	Benjamin W. Richards
1779	
Matthew Clarkson	1852 to 1874, inclusive
	Charles B. Trego
(No minutes for 1780)	
1781 to 1790, inclusive	1875 to 1897, inclusive
Francis Hopkinson	J. Sergeant Price

1898 to 1902, inclusive
Horace Jayne

1903 to 1920, inclusive
Henry La Barre Jayne

1921 to 1932, inclusive
Eli Kirk Price

1933, March to May
William P. Gest (to fill the
vacancy created by the
death of Eli Kirk Price)

1933-
Fidelity-Philadelphia Trust
Company

COUNCILLORS

(All councillors elected for three
years except when otherwise
indicated)

1781

George Bryan
Thomas McKean
Barbe De Marbois
Charles Thomson
For two years
George Duffield
William Livingston
Thomas Jefferson
John Witherspoon
For one year
Ezra Stiles
Matthew Clarkson
Jonathan B. Smith
John Lukens

1782

Joseph Reed
Jonathan B. Smith
Jared Ingersoll
Owen Biddle

1783

Thomas Jefferson
John Witherspoon
George Duffield
David Rittenhouse

1784

Thomas McKean
George Bryan
Barbe De Marbois
Samuel Caldwell

1785

Jared Ingersoll
Jonathan B. Smith
Joseph Reed
Robert Blackwell

1786

David Rittenhouse
Benjamin Rush
John Jones
Adam Kuhn (to fill the va-
cancy created by the death
of Joseph Reed)
George Duffield

1787

Thomas McKean
George Bryan
Samuel Caldwell
Jonathan Hoge

1788

Jared Ingersoll
Robert Blackwell
Adam Kuhn
Charles Pettit

1789

Charles Pettit
Benjamin Rush
John Jones
George Duffield

1790

Thomas McKean
Robert Blackwell
William Barton
Isaac Gray

1791

Adam Kuhn
Jared Ingersoll
Andrew Ellicott
Samuel P. Griffiths
For one year
Nicholas Collin (to fill the
vacancy created by the
death of George Duffield)
For unexpired terms
Thomas McKean
Robert Blackwell
William Barton
Charles Pettit
Isaac Gray
Benjamin Rush
John Jones

1792

Charles Pettit
Nicholas Collin
Benjamin Rush
William White

1793

J. Thornton
Thomas McKean
William Barton
Robert Blackwell

1794

Jonathan Williams, Jr.
John Andrews
Andrew Ellicott
Samuel P. Griffiths
James Davidson (to fill the
vacancy created by the
death of William Barton)

1795

William Smith
Jonathan B. Smith
William Currie
William White

1796

Robert Blackwell
Thomas McKean
James Davidson
Adam Kuhn

1797

Andrew Ellicott
Tench Coxe
James Abercrombie
Richard Peters Smith

1798

Jonathan B. Smith
William Smith
William Currie
Samuel Wheeler
Jonathan Williams, Jr. (to
fill the vacancy created by
the death of Richard Peters
Smith)

1799

Thomas McKean
James Davidson
Robert Blackwell
Adam Kuhn

1800

Jonathan Williams, Jr.
 Andrew Ellicott
 Tench Coxe
 Samuel Magaw
For two years
 Benjamin H. Latrobe (to fill
 the vacancy created by
 Thomas McKean, becoming
 Patron of the Society)

1801

Jonathan B. Smith
 William Currie
 Samuel Wheeler
 Peter Stephen Du Ponceau

1802

James Woodhouse
 John Bleakley
 Benjamin H. Latrobe
 Samuel Duffield

1803

Jonathan Williams, Jr.
 Andrew Ellicott
 Samuel Magaw
 Nicholas Collin
For two years
 Tench Coxe (to fill the va-
 cancy created by the death
 of John Bleakley)

1804

William White
 Jonathan B. Smith
 Peter Stephen Du Ponceau
 Adam Kuhn

1805

James Woodhouse
 Samuel Duffield

William Shippen
 Zaccheus Collins

1806

Benjamin Rush
 Andrew Ellicott
 Nicholas Collin
 William Tilghman

1807

William White
 Peter Stephen Du Ponceau
 Jonathan Williams, Jr.
 William Short

1808

John McDowell
 Zaccheus Collins
 James Woodhouse
 William Shippen

1809

Nicholas Collin
 Andrew Ellicott
 Benjamin Rush
 William Tilghman
For two years
 Jonathan B. Smith (to fill the
 vacancy created by the
 death of William Shippen)

1810

Peter Stephen Du Ponceau
 Jonathan Williams, Jr.
 Mahlon Dickerson
 William White
For one year
 Adam Seybert (to fill the
 vacancy created by the
 death of James Wood-
 house)

1811

Adam Seybert
Jonathan B. Smith
James Gibson
J. H. Brinton

1812

Nicholas Collin
Benjamin Rush
William Tilghman
Andrew Ellicott

1813

William White
Peter Stephen Du Ponceau
Jonathan Williams, Jr.
Horace Binney
For one year
Edward Penington (to fill
the vacancy created by the
death of Jonathan B.
Smith)

1814

Thomas Cooper
James Gibson
Edward Penington
Robert Hare, Jr.
For one year
William Meredith (to fill the
vacancy created by the
death of Benjamin Rush)

1815

Nicholas Collin
William Tilghman
Andrew Ellicott
William Meredith

1816

William White
Horace Binney

John Sergeant
William Rawle

1817

Thomas Cooper
James Gibson
Nathaniel Chapman
Samuel Calhoun
For one year
William Hembel, Jr. (to fill
the vacancy created by the
election of William Tilgh-
man as vice-president of
the Society)

1818

Thomas Jefferson
William Maclure
Nicholas Collin
William Meredith

1819

William Rawle
Horace Binney
John Sergeant
John Quincy Adams

1820

James Gibson
Nathaniel Chapman
Robert Hare, Jr.
William Hembel, Jr.

1821

Thomas Jefferson
William Maclure
Nicholas Collin
William Meredith

1822

Horace Binney
John Quincy Adams
John Sergeant
William Rawle

1823

Nathaniel Chapman
Robert Hare, Jr.
William Hembel, Jr.
Clement C. Biddle

1824

Thomas Jefferson
William Maclure
Nicholas Collin
William Meredith

1825

Horace Binney
John Sergeant
John Quincy Adams
William Rawle

1826

Nathaniel Chapman
William Hembel, Jr.
Robert Hare, Jr.
Clement C. Biddle

1827

William Meredith
Nicholas Collin
William Maclure
Robert Walsh, Jr.

1828

John Quincy Adams
John Sergeant
William Short
Samuel Moore
For one year
Robert Adrain (to fill the
vacancy created by the
election of Nathaniel
Chapman as vice-president
of the Society)

1829

Robert Hare, Jr.
William Rawle
Joseph Hopkinson
William Hembel, Jr.

(No minutes for 1830)

1831

Nicholas Biddle
Nicholas Collin
William Meredith
For one year

William H. Keating (to fill
the vacancy created by the
election of Joseph Hopkin-
son as vice-president of the
Society)

1832

William Hembel, Jr.
William Rawle
Robert Hare, Jr.
Charles D. Meigs
For two years

James Mease (to fill the
vacancy created by the
death of Nicholas Collin)

1833

William Short
Clement C. Biddle

1834

Nicholas Biddle
William H. Delancey
Thomas Biddle
James Mease

1835

William Rawle
Robert Hare, Jr.
William Hembel, Jr.
Eugenius Nulty

- 1836
 William Short
 George Ord
 William H. Keating
 Clement C. Biddle
- 1837
 Nicholas Biddle
 Thomas Biddle
 James Mease
 Gouverneur Emerson
For one year
 Joshua Francis Fisher (to fill
 the vacancy created by the
 death of William Rawle)
- 1838
 Robert Hare, Jr.
 William Hembel, Jr.
 William Meredith
 Charles D. Meigs
- 1839
 William Short
 William H. Keating
 George Ord
 Clement C. Biddle
- 1840
 Nicholas Biddle
 Thomas Biddle
 Gouverneur Emerson
 Joshua Francis Fisher
- 1841
 Robert Hare, Jr.
 William Hembel, Jr.
 Charles D. Meigs
 Henry Vethake
For one year
 Joseph Henry (to fill the
 vacancy created by the
- death of William H. Keating)
- 1842
 Clement C. Biddle
 William Short
 Joseph Henry
 Philip H. Nicklin
- 1843
 Thomas Biddle
 Gouverneur Emerson
 Isaac Lea
 Hartman Kuhn
For two years
 Benjamin Dorr (to fill the
 vacancy created by the
 death of Philip H. Nicklin)
- 1844
 Robert Hare, Jr.
 William Hembel, Jr.
 Charles D. Meigs
 Henry Vethake
- 1845
 Clement C. Biddle
 Benjamin Dorr
 William Short
 Joseph Henry
- 1846
 Thomas Biddle
 Isaac Lea
 Hartman Kuhn
 Thomas P. Cope
- 1847
 Robert Hare, Jr.
 William Hembel, Jr.
 Charles D. Meigs
 Henry Vethake

1848

Clement C. Biddle
William Short
Joseph Henry
Benjamin Dorr

1849

Thomas Biddle
Isaac Lea
Hartman Kuhn
Alfred Langdon Elwyn

1850

Robert Hare, Jr.
William Hembel, Jr.
Charles D. Meigs
Henry Vethake
For one year
George M. Justice (to fill the
vacancy created by the
death of William Short)

1851

Clement C. Biddle
George M. Justice
Frederick Fraley
Henry Reed

1852

Thomas Biddle
Isaac Lea
Hartman Kuhn
Alfred Langdon Elwyn
For one year
Isaac Hays (to fill the va-
cancy created by the death
of William Hembel, Jr.)

1853

Isaac Hays
Charles D. Meigs
Henry Vethake
Jacob G. Morris

1854

Clement C. Biddle
George M. Justice
Frederick Fraley
Henry Reed

1855

Thomas Biddle
Isaac Lea
Alfred Langdon Elwyn
John Bell
For two years
George Tucker (to fill the
vacancy created by the
death of Henry Reed)
For one year
Robert Bridges (to fill the
vacancy created by the
death of Jacob G. Morris)

1856

Isaac Hays
Charles D. Meigs
Henry Vethake
Robert Bridges

1857

George M. Justice
George Tucker
William Harris
Robert Patterson

1858

Alfred Langdon Elwyn
John Bell
Henry Coppée
Edward King

1859

Isaac Hays
Robert E. Rogers
Henry C. Carey
Robert Bridges

- 1860
George M. Justice
George Tucker
Robert Patterson
Henry Vethake
- 1861
Alfred Langdon Elwyn
John Bell
Henry Coppée
Edward King
For two years
Frederick Fraley (to fill the
vacancy created by the
resignation of George M.
Justice)
- 1862
Isaac Hays
Robert E. Rogers
Henry C. Carey
Robert Bridges
- 1863
Frederick Fraley
Robert Patterson
Daniel R. Goodwin
William Parker Foulke
- 1864
Alfred Langdon Elwyn
John Bell
Henry Coppée
Oswald Thompson
- 1865
Isaac Hays
Robert E. Rogers
Henry C. Carey
Robert Bridges
- 1866
Frederick Fraley
Robert Patterson
- Daniel R. Goodwin
Eli K. Price
- 1867
Alfred Langdon Elwyn
John Bell
Benjamin H. Coates
Benjamin V. Marsh
- 1868
Isaac Hays
Robert E. Rogers
Henry C. Carey
Robert Bridges
- 1869
Frederick Fraley
Robert Patterson
Daniel R. Goodwin
Eli K. Price
- 1870
Alfred Langdon Elwyn
John Bell
Benjamin H. Coates
Benjamin V. Marsh
- 1871
Isaac Hays
Robert E. Rogers
Henry C. Carey
Robert Bridges
- 1872
Daniel R. Goodwin
Eli K. Price
W. S. W. Ruschenberger
Henry Winsor
- 1873
Alfred Langdon Elwyn
Benjamin H. Coates
Pliny E. Chase
Benjamin V. Marsh

1874

Isaac Hays
Robert E. Rogers
Henry C. Carey
Robert Bridges

1875

Daniel R. Goodwin
Eli K. Price
W. S. W. Ruschenberger
Henry Winsor

1876

Alfred Langdon Elwyn
Benjamin H. Coates
Benjamin V. Marsh
George H. Horn

1877

Isaac Hays
Robert E. Rogers
Henry C. Carey
Robert Bridges

1878

Daniel R. Goodwin
W. S. W. Ruschenberger
Henry Winsor
William A. Ingham

1879

Alfred Langdon Elwyn
Benjamin H. Coates
Benjamin V. Marsh
George H. Horn

1880

Robert E. Rogers
Robert Bridges
Oswald Seidensticker
Richard Wood

1881

Daniel R. Goodwin
W. S. W. Ruschenberger
Henry Winsor
William A. Ingham

1882

Alfred Langdon Elwyn
Benjamin V. Marsh
Aubrey H. Smith
George R. Morehouse

1883

Robert E. Rogers
Oswald Seidensticker
Richard Wood
Philip H. Law
For two years
Charles A. Ashburner (to fill
the vacancy created by the
death of Benjamin V.
Marsh)

1884

Daniel R. Goodwin
W. S. W. Ruschenberger
Henry Winsor
William A. Ingham

1885

Aubrey H. Smith
George R. Morehouse
Charles A. Ashburner
Edward D. Cope
For one year
Persifor Frazer, Jr. (to fill the
vacancy created by the
death of Robert E. Rogers)

1886

Oswald Seidensticker
Richard Wood

- William V. McKean
Persifor Frazer, Jr.
For one year
Thomas H. Dudley (to fill the
vacancy created by the
resignation of W. S. W.
Ruschenberger)
- 1887
Daniel R. Goodwin
Henry Winsor
William A. Ingham
Thomas H. Dudley
For two years
Richard Vaux (to fill the
vacancy created by the
resignation of Oswald
Seidensticker)
- 1888
Aubrey H. Smith
J. Cheston Morris
Edward D. Cope
George R. Morehouse
- 1889
Richard Wood
William V. McKean
Richard Vaux
Isaac C. Martindale
For two years
Samuel Wagner (to fill the
vacancy created by the
resignation of J. Cheston
Morris)
- 1890
Daniel R. Goodwin
William A. Ingham
Thomas H. Dudley
Robert Patterson
- 1891
Aubrey H. Smith
George R. Morehouse
Samuel Wagner
William C. Cattell
For two years
Charles S. Wurts (to fill the
vacancy created by the
death of Daniel R. Good-
win)
- 1892
Richard Wood
William V. McKean
Richard Vaux
Isaac C. Martindale
For two years
William P. Tatham (to fill
the vacancy created by the
death of Aubrey H. Smith)
- 1893
William A. Ingham
Thomas H. Dudley
Robert Patterson
Charles S. Wurts
For two years
Henry C. Baird (to fill the
vacancy created by the
death of Isaac C. Martin-
dale)
- 1894
William P. Tatham
George R. Morehouse
Samuel Wagner
William C. Cattell
For two years
Henry Hartshorne (to fill the
vacancy created by the
death of Thomas H.
Dudley)

1895

Richard Wood
William V. McKean
Richard Vaux,
Henry C. Baird

1896

William A. Ingham
Charles S. Wurts
Robert Patterson
Henry Hartshorne
For two years
Isaac J. Wistar (to fill the
vacancy created by the
death of Richard Vaux)

1897

George R. Morehouse
William C. Cattell
William P. Tatham
Patterson Du Bois

1898

Richard Wood
Henry C. Baird
Isaac J. Wistar
Jacob M. Da Costa
For one year
George F. Edmunds (to fill
the vacancy created by the
death of Henry Harts-
horne)

1899

William A. Ingham
Charles S. Wurts
George F. Edmunds
James T. Mitchell
For one year
Henry C. Trumbull (to fill
the vacancy created by the
death of William C. Cat-
tell)

1900

George R. Morehouse
Patterson Du Bois
Henry C. Trumbull
Charles L. Doolittle

1901

Richard Wood
Henry C. Baird
Samuel G. Dixon
Joseph G. Rosengarten

1902

Albert H. Smyth
George F. Edmunds
James T. Mitchell
Joseph Wharton

1903

George R. Morehouse
Patterson Du Bois
Ira Remsen
Isaac J. Wistar

1904

Richard Wood
Henry C. Baird
Samuel G. Dixon
Joseph G. Rosengarten

1905

George F. Edmunds
James T. Mitchell
Joseph Wharton
William W. Keen

1906

Patterson Du Bois
Samuel Dickson
Ernest W. Brown
William Keith Brooks

- 1907
 Richard Wood
 Samuel G. Dixon
 Joseph G. Rosengarten
 Henry Fairfield Osborn
- 1908
 Hampton L. Carson
 Talcott Williams
 Harry F. Keller
 Francis B. Gummere
- 1909
 Charlemagne Tower
 Robert S. Woodward
 William Gilson Farlow
 R. A. F. Penrose, Jr.
- 1910
 Edward L. Nichols
 Samuel Dickson
 Ernest W. Brown
 Morris Jastrow, Jr.
- 1911
 Henry Fairfield Osborn
 Joseph G. Rosengarten
 Edward W. Morley
 Henry H. Donaldson
- 1912
 William Trelease
 Francis B. Gummere
 Robert Williams Wood
 John Frederick Lewis
- 1913
 Charlemagne Tower
 William Morris Davis
 George Ellery Hale
 R. A. F. Penrose, Jr.
For two years
 Samuel W. Pennypacker (to
 fill the vacancy created by
- the resignation of John
 Frederick Lewis)
- 1914
 Samuel Dickson
 Ernest W. Brown
 Morris Jastrow, Jr.
 Arthur Gordon Webster
- 1915
 Henry H. Donaldson
 Theodore W. Richards
 Robert A. Harper
 Edwin G. Conklin
- 1916
 Louis A. Bauer
 Edward P. Cheyney
 Russell H. Chittenden
 Charles D. Walcott
- 1917
 Henry Fairfield Osborn
 Elihu Thomson
 Samuel M. Vauclain
 Henry B. Fine
- 1918
 Bertram B. Boltwood
 Ernest W. Brown
 Francis B. Gummere
 Herbert S. Jennings
- 1919
 Maurice Bloomfield
 John M. Clarke
 George H. Parker
 Arthur G. Webster
- 1920
 William Libbey
 William W. Atterbury
 Michael I. Pupin

- Morris Jastrow, Jr.
For one year
 Edwin Swift Balch (to fill the
 vacancy created by the
 death of Francis B. Gum-
 mere)
- 1921
 Bradley M. Davis
 William C. Farabee
 John Frederick Lewis
 Edwin Bidwell Wilson
- 1922
 Lafayette B. Mendel
 Herbert S. Jennings
 William W. Campbell
 Robert A. Millikan
For one year
 Felix E. Schelling (to fill the
 vacancy created by the
 death of Morris Jastrow,
 Jr.)
- 1923
 John C. Merriam
 James H. Breasted
 Ambrose Swasey
 Henry G. Bryant
- 1924
 Henry Crew
 Samuel W. Stratton
 William E. Lingelbach
 Victor C. Vaughan
- 1925
 Thomas B. Osborne
 John Frederick Lewis
 William M. Wheeler
 William Trelease
- 1926
 Herman V. Ames
 Whitman Cross
 Walton B. McDaniel
 Oswald Veblen
- 1927
 Edwin G. Conklin
 Cyrus Adler
 William C. Sproul
 Charles F. Brush
- 1928
 Henry H. Donaldson
 Russell Duane
 Herbert S. Jennings
 Arthur E. Kennelly
- 1929
 Charles B. Davenport
 William H. Hobbs
 Emory R. Johnson
 Harlow Shapley
- 1930
 William B. Scott
 John Frederick Lewis
 Dana C. Munro
 Edwin Bidwell Wilson
- 1931
 James M. Beck
 Francis G. Benedict
 Lafayette B. Mendel
 Edwin G. Conklin
- 1932
 Cyrus Adler
 Henry H. Donaldson
 Herbert S. Jennings
 William Lyon Phelps
For two years
 Heber D. Curtis (to fill the
 vacancy created by the

election of Edwin G. Conklin as vice-president of the Society)	1934	Charles G. Abbot
		James A. Montgomery
		John Cadwalader
		Hugh S. Taylor
1933		
Frank Schlesinger	1934—December	
Edward W. Berry		Russell Duane (to fill the
Frank P. Graves		vacancy created by the
Gilbert A. Bliss		death of John Cadwalader)

LIBRARIANS

- David Rittenhouse, January 28, 1775 – d. June 26, 1796.
 John Vaughan, March 18, 1803 – d. December 30, 1841.
 George Ord, January 21, 1842 – January 21, 1848.
 Charles B. Trego, January 21, 1848 – January 15, 1858.
 J. Peter Lesley, January 15, 1858 – January 16, 1885.
 Henry Phillips, Jr., January 16, 1885 – d. June 6, 1895.
 George H. Horn, *pro tem*, September 20, 1895 – January 17, 1896;
 January 17, 1896 – d. November 24, 1897.
 Isaac Minis Hays, *pro tem*, January 15, 1897 – January 21, 1898;
 January 21, 1898 – resigned, April 22, 1922.



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